FORMULAS AND TABLES TO FACILITATE THE CALCULATION OF RECOMBINATION VALUES IN HEREDITY[1]

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THE MOST USEFUL METHODS for estimating recombination values in heredity are the product moment method and the method of maximum likelihood (Fisher and Balmukand, 1928). The product method is simple to apply in conjunction with tables such as those calculated by Immer (1930), Stephens (1939), and Immer and Henderson (1943), but the method is limited to cases where 4-class segregations occur. The method of maximum likelihood, on the other hand, is quite general and may be applied to any genetic data providing information about linkage. The method is also applicable if more than one type of data is available.

When such complex data are encountered, the estimation of the recombination value and the examination of heterogeneity are both facilitated by the use of scores based on the method of maximum likelihood (Fisher, 1946). In connection with linkage investigations at the University of California, Davis, over the past several years, maximum-likelihood equations have been derived for a wide variety of genetic situations, and tables of scores have been calculated to facilitate the solutions of these equations. Formulas for the calculation of standard errors of recombination values have also been derived and tables prepared facilitating their calculation. The purpose of this paper is to make these equations and tables generally available and to provide a numerical example of their use. Because of the importance of planning in linkage experiments, the use of the tables for this purpose is described.

Mather (1935, 1951) has discussed in detail the combination of data in estimating recombination values. In brief, the method requires that the logarithms of the probabilities of obtaining the observed families be maximized with respect to the parameters to be estimated; this is accomplished by differentiating partially with respect to each parameter in turn, equating the derivatives to zero, and solving the resulting set of simultaneous equations. Assuming that the various sets of data pertain to a single recombination value, the estimation equation takes the form

$$\frac{dL}{dp} = a_1 \frac{d \log m_1}{dp} + a_2 \frac{d \log m_2}{dp} + \cdots + a_t \frac{d \log m_t}{dp} = 0 ,$$

[235]

where p represents the recombination fraction, a_1 and m_1 the observed and expected numbers, respectively, in the first of the t distinguishable classes, etc.[3] The use of scores in the solution of estimation equations depends upon

the fact that $\dfrac{d \log m_1}{dp}$, $\dfrac{d \log m_2}{dp}$, etc., each have a unique value for any

given p, this value (or score) representing the contribution one individual in a particular class makes to the derivative of the logarithm of the likelihood expression. The product obtained by multiplying this score by the observed number in a class gives the total contribution (or total score) of the class to the derivative. The solution of the equation is clearly provided by the value of p for which the total scores sum to zero.

The symbols used to represent the observed and expected frequencies for various genotypes and phenotypes can be found in tables 4 and 5. It has been convenient to follow Immer (1934) in using the symbols $a, b, c \ldots \ldots$ to represent observed frequencies. Estimation equations for a variety of types of genetic families are summarized in table 6, and scores for the majority of the classes likely to be encountered in linkage studies are in table 7. In the text and table 6, certain types of families are identified by the ratios they produce when $p = 0.50$, that is, when the genes involved are independent. Lack of suitable terminology made this necessary.

It can be shown that the mean amount of information, i_p, supplied by a single individual in an F_2 family (or by a single F_3 family) is given by

$$i_p = - \sum \left(m \frac{d^2 \log n}{dp^2} \right) \text{ or alternatively by } i_p = \sum \left[\frac{1}{m} \left(\frac{dm}{dp} \right)^2 \right]. \text{ Since } i_p$$

depends only on the value of p, it is readily tabulated and need only be multiplied by n, the number of individuals in the family, to obtain I_p, the total amount of information provided by the F_2 family. I_p is the inverse of the

variance so that $V_p = \dfrac{1}{I_p}$. Hence the standard error of p is

$$s_p = \sqrt{V_p} = \sqrt{\frac{1}{I_p}} = \sqrt{\frac{1}{n i_p}}.$$

Mean amounts of information (i_p) supplied by a single F_2 individual in a number of types of families at various values of p are in table 8.

APPLICATION OF THE TABLES

The application of the tables can be illustrated by using some unpublished data from lima beans. The genes involved are D vs. d (determinate vs. indeterminate growth habit) and R vs. r (dark red vs. red seed coat) (Allard, 1953a and b).

The first data concerning the linkage relations of these gene pairs to become available were the three sets of F_2 coupling data shown in table 1. These data suggested that the two gene pairs might be linked. Accordingly, a

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[3] Throughout this paper "log" means "log$_e$."

precise test for independence was made by a χ^2 analysis. The χ^2 value associated with interaction was highly significant, indicating linkage. The recombination value was then calculated by the product method and found to be 41 ± 1.42 per cent. Further, it was determined by a 3×4 contingency table that the data are homogeneous. Over a period of several years additional data concerning linkage between these gene pairs became available, mostly incidental to other studies. Finally the nine bodies of data summarized in table 1 were at hand for the estimation of the recombination value. The data represent six different parental combinations grown in five different seasons. It should be noted that these data include six different types of genetic families.

Once these various bodies of data were available, it became desirable, of course, to use all of them in determining the recombination value. The first step of this process requires that the observed values in table 1 be substituted in the appropriate estimation equation from table 6. For example, the equation for the two sets of F_2 repulsion data is number 6. When the observed values for the fourth set of data in table 1 are substituted, the estimation equation becomes

$$293 \left(\frac{2p}{2 + p^2} \right) + 226 \left(\frac{-2p}{1 - p^2} \right) + 35 \left(\frac{2}{p} \right) = 0 .$$

Similarly, the estimation equation for the first set of coupling-phase data is

$$200 \left[\frac{2(p - 1)}{3 - 2p + p^2} \right] + 106 \left[\frac{2(1 - p)}{p(2 - p)} \right] + 30 \left(\frac{2}{p - 1} \right) = 0 .$$

This equation was obtained by substituting $1 - p$ for p in equation 6 and reversing the sign. All equations in table 6 and elsewhere are given for repulsion phase, and the substitution of $1 - p$ for p (accompanied by the sign change) must be made for all coupling data if both repulsion and coupling data are to be combined. If only the coupling phase is concerned, the repulsion-phase equations can be used and the answer subtracted from unity to obtain the p value. Estimation equations for the seven other sets of data can be obtained in a similar manner from tables 1 and 6.

The nine estimation equations should then be evaluated at $p = 0.50$. This evaluation is easily accomplished with the scores in table 7. The amount of information provided by each body of data is obtained by finding the mean amount of information contributed per individual at $p = 0.50$, in table 8, and multiplying by the number of individuals. The scores and I_p values for each of the nine sets of data are summarized in table 2. The consistently negative values for the total scores indicate that the trial value of $p = 0.50$ is too high.

The next trial value of p can be obtained by Newton's method. In this method the deviation from zero of the first derivative (that is, the sum of the total scores) is divided by the second derivative (I_p) to estimate the correction to be made in p. Thus at $p = 0.50$ the sum of all the remainders divided by the total information is found to be

$$\frac{-649.778}{5826.488} = -0.112 ,$$

giving $0.50-0.11 = 0.39$ as a provisional estimate of p. Two additional applications of this process, as shown in table 2, establish that p slightly exceeds 0.40. Accepting $p = 0.40$ as sufficiently accurate, the standard error of this estimate is obtained by taking the square root of the inverse of the amount of information:

$$s_p = \sqrt{\frac{1}{6807.455}} = 0.012 \ .$$

Thus, the recombination value is estimated as 40 ± 1.2 per cent.

Only one question remains to be answered: Are the data consistent in supporting this recombination value? Fisher (1949) has shown that the sum of the squares of the deviations from zero of the logarithm of the maximum-likelihood expression for each body of data, divided by the total amount of information provided by that body of data, is distributed as χ^2. Thus,

$$\chi^2 = \sum_1^N \frac{D^2}{I}$$

will provide a homogeneity test with $N - 1$ degrees of freedom (N = number of sets of data pooled). Applied to the present example (see table 2),

$$\chi^2 = \frac{(-2.9449190)^2}{765.408} + \frac{(68.7393910)^2}{3319.046} + \cdots + \frac{(-10.5278834)^2}{59.983} = 39.581 \ .$$

Part of this value comes from the over-all deviation from expectancy resulting from the fact that p was not estimated perfectly. This portion of the total χ^2 can be estimated as $\dfrac{(16.6886852)^2}{6807.455} = 0.041$. The remainder, 39.540, measures the homogeneity of the nine sets of data. This χ^2 value has eight degrees of freedom and is obviously significant. The data therefore do not agree in supporting the hypothesis that the recombination value is 40 per cent.

Recombination values were then calculated for each set of data individually with the results shown in table 3. All of the recombination values were lower than 0.50, and with but two exceptions the deviations from independence were significant. The fact that the two loci are linked is therefore established beyond reasonable doubt. The data do not agree, however, in supporting the hypothesis that the recombination value is the same in the different tests. Most of the difficulty stems from three sets of data, numbers 4, 5, and 6. The different recombination values observed in these cases could have been the result of seasonal influences upon recombination values, differences among the parental strains used, different recombination values in the sexes, or a combination of these factors. For purposes of prediction, the recombination fraction of $p = 0.40$ appears to be the most appropriate, but defections from this value in certain seasons or with some parental combinations must be recognized as a possibility.

It will have been noticed that the maximum number of significant figures provided by tables 7 and 8 was carried in this example. This was done to avoid any possible confusion in extracting values from the tables. The inves-

tigator can determine the appropriate number of significant figures for any particular case from the formulas given as footnotes to these tables. The number of significant figures in tables 7 and 8 was selected to provide at least 3-figure accuracy in final recombination values and standard errors for most data likely to be encountered. They provide less accuracy under some circumstances, particularly when the number of scores combined is large or when information values are small.

This example illustrates the use of (a) scores for solving maximum-likelihood equations, (b) tables of i_p values for calculating standard errors, and (c) heterogeneity tests when several sorts of data are combined. An ancillary use of the i_p tables is in the planning of linkage experiments. Their use in predicting the value of various sorts of data for the estimation of linkage is discussed in the following section.

PLANNING LINKAGE EXPERIMENTS
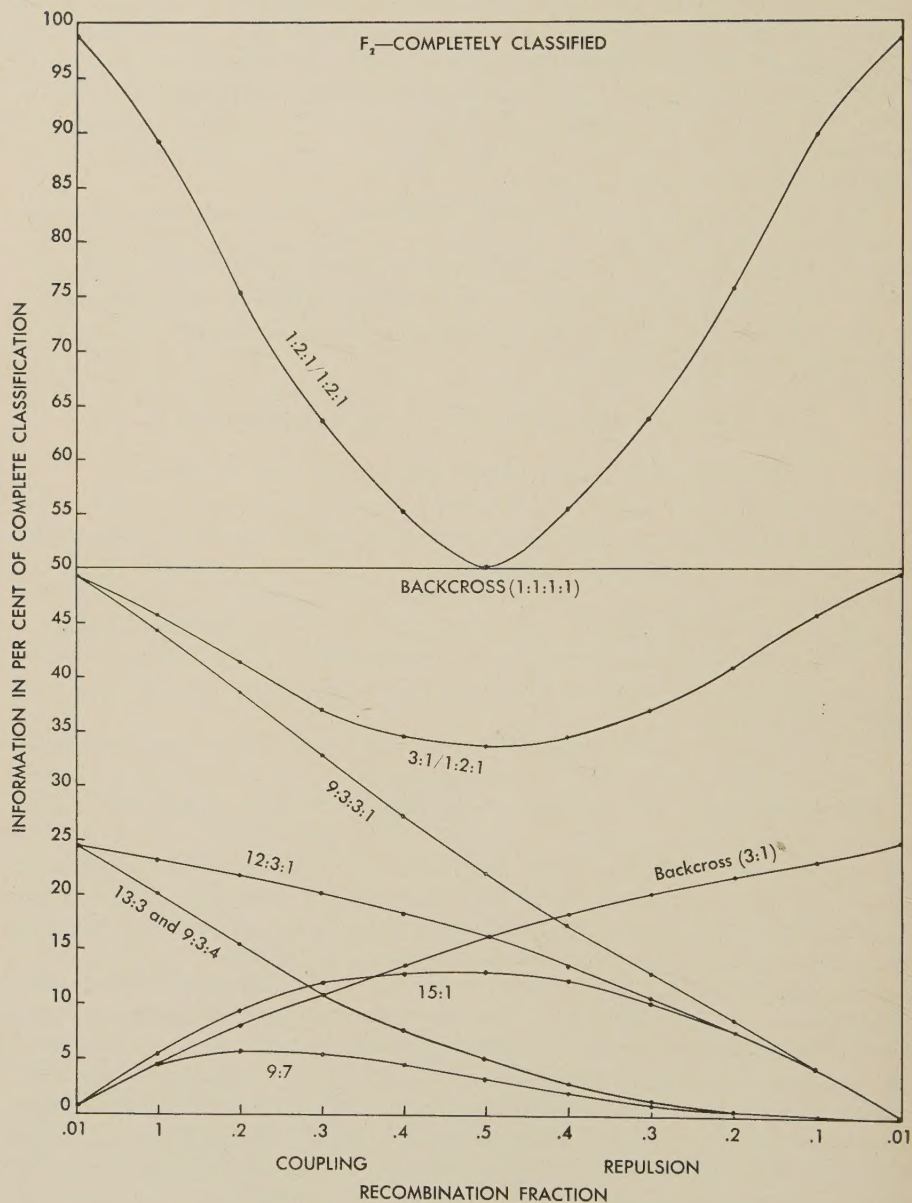
Linkage Estimates from Backcross and F_2 Data

The amount of information about the recombination fraction provided by any set of data depends upon two factors: the completeness of the classification and the closeness of the linkage. No type of progeny segregating for two pertinent genes gives more information per individual than an F_2 completely classified into the 10 possible genotypes. For this reason complete classification will be used here as a standard for comparing the value of different sorts of data, even though complete classification can only rarely be achieved without progeny tests.

With complete classification the amount of information per individual varies strikingly with changes in the magnitude of p. At $p = 0.50$ each individual contributes 8 units of information about p (table 8). Amounts of information per individual gradually increase as p becomes smaller until at $p = 0.01$ each individual contributes more than 200 units of information about p, or more than 25 times more information than is obtained with independence. These absolute amounts of information should be borne in mind in comparing data from complete classification with other types of data.

The magnitude of i_p in the usual backcross, that is, the backcross in which four classes are recognizable, is exactly one half that of complete classification. This is easily understandable since the value of p in the F_2 is influenced by crossing-over in both sexes. This does not mean that F_2 data are more useful than backcross data. Backcrosses allow the separate estimation of crossing-over in both sexes. Hence they are almost always to be preferred to F_2's if they can be obtained with reasonable economy, since with F_2 data crossing-over must be assumed to be equal in both sexes.

With certain types of interallelic interaction, for example, with complementary genes, only two classes appear in the backcross of the double heterozygote to the double recessive. When the expected ratio is $1 + p: 1 - p$, that is, $3:1$ when $p = 0.50$, backcrosses provide only one fourth as much information per individual as complete classification (table 8). It is apparent from this table that such backcrosses in close repulsion are virtually valueless in the measurement of linkage.

The previous case illustrates the fact that a reduction in the number of

F₂—COMPLETELY CLASSIFIED

1.2.1/1.2.1

BACKCROSS(1:1:1:1)

3:1/1:2:1

9:3.3:1

12:3:1

Backcross (3:1)

13:3 and 9:3:4

15:1

9:7

COUPLING   REPULSION

RECOMBINATION FRACTION

INFORMATION IN PER CENT OF COMPLETE CLASSIFICATION

recognizable classes in backcrosses is accompanied by a reduction in the amount of information and that the loss is dependent upon the linkage intensity. This situation also prevails in F_2 where the losses resulting from incomplete classification may be severe. The value of i_p for a number of the common F_2 ratios is given in table 8. The comparative efficiency of various sorts of data is probably most readily visualized in a diagram such as figure 1 in which various sorts of backcross and F_2 data are compared with complete classification as a standard. In general, the losses of information caused by incomplete classification are greatest in repulsion. This fact should be kept in mind in planning linkage experiments.

It should also be kept in mind that figure 1 compares the *relative* efficiency of various sorts of progenies with complete classification. Usually the investigator has no choice in the type of progeny he must use, and his primary interest resides in the practicality of estimating linkage from the sort of data he has or can obtain conveniently. Given the approximate cross-over value, table 8 makes it possible to estimate rapidly the size of population required for a given degree of accuracy. Thus, if dominance is complete at both loci, the cross is one of repulsion, p is believed to be approximately 0.05, and a standard error not larger than 5 per cent is required, $n = (i_p \sigma^2)^{-1} = [(1.006)(0.05)^2]^{-1} = 398$.

This is a reasonable population size in most plant species. However, if all of the above postulates apply except that linkage between complementary genes is to be measured, n becomes 133,000, an impractically large number. If efficiency were not considered in advance in this latter case, a fairly standard population of 500 plants would provide a standard error of 82 per cent, indicating clearly that the estimate of p obtained would be meaningless.

The Use of Progeny Tests

In the previous section it was established that the loss of information resulting from incomplete classification in the F_2 can be very large. In some instances the losses due to this cause can be so large as to make the F_2 virtually valueless in the measurement of linkage. This being the case, progeny tests of F_2 individuals might prove more fruitful than raising additional F_2's. In the following sections the relative value of F_2 and F_3 data is considered for the more common genetic situations. It should be emphasized that all calculations are based on the assumption of easy recognition of the various phenotypes in F_2. This is frequently not the case, as for example when one or both of the gene pairs governs disease resistance. Here classification of single F_2 plants is frequently difficult, but if F_3 families are grown, the genotype of F_2 plants can often be identified with assurance. Under such circumstances progeny tests are comparatively more valuable than indicated in the calculations to follow. A graphic comparison of the efficiency of various types of data is provided in figure 2.

The case of incomplete dominance. With both gene pairs expressing incomplete dominance, progeny tests provide two sorts of information, that obtained from completing, partially or completely, the F_2 classification, that is, separating AB/ab from Ab/aB, and that resulting from the fact that each F_3 progeny is equivalent to an F_2. Each family identified as to linkage
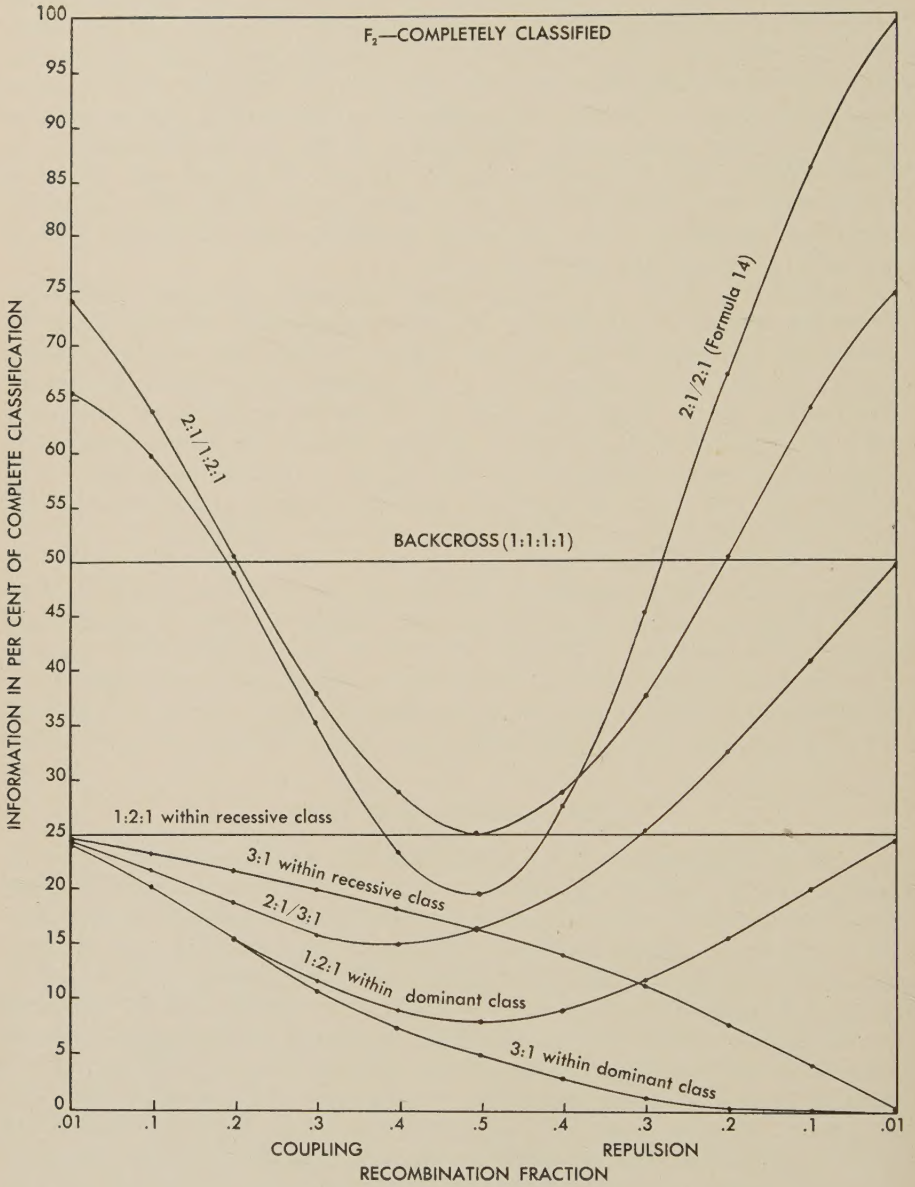
phase contributes $4/(1 - 2p + 2p^2)^2$ units of information about p in connection with the separation of AB/ab from Ab/aB and, in addition, F_2 type of information from either coupling or repulsion phase. These three sorts of data can, of course, be combined with the original F_2 data to find the recombination value providing the best over-all fit.

In general outline, the procedure to be followed requires the estimation of p for each family in order to separate coupling and repulsion progenies. The values of p thus calculated would be expected to be normally distributed about the true value of p. It is possible, however, to determine the number of progeny that will serve to differentiate the repulsion and coupling cases at any prescribed level of probability. Achieving accurate classification in 99 out of 100 cases would appear to be satisfactory in most linkage investigations. Hence this level of probability will be used here and subsequently in connection with progeny tests.

The number of individuals required per family to assign it unambiguously $(P = 0.99)$ to one or the other linkage phase is given by

$$n = \left\{ \frac{2.58 \left[\sqrt{\dfrac{(p - p^2)(1 - 2p + 2p^2)}{2(1 - 3p + 3p^2)}} + \sqrt{\dfrac{(q - q^2)(1 - 2q + 2q^2)}{2(1 - 3q + 3q^2)}} \right]}{q - p} \right\}^2 .$$

This method was first proposed by Immer (1934) for the solution of some similar problems. The number of plants required per progeny turns out to be 22 at $p = 0.30$ and 89 at $p = 0.40$.

The advantage of progeny tests over raising additional F_2 individuals rests entirely with the additional information gained from completing the classification. Hence, if large families must be grown, comparatively few can be raised, and little information will be gained by completing the classification. Also, certain families may be misclassified as to their origin from coupling or repulsion F_2 individuals, with the result that use of the F_2 type of data can lead to error. In view of these factors, it would not seem desirable to attempt progeny tests at values of p much larger than 0.30. At lower values of p they are more useful than raising additional F_2 individuals.

The problem discussed here is largely academic because of the rarity of cases involving incomplete dominance for both gene pairs and also because the great efficiency of such data in F_2 will usually provide a small standard error without recourse to progeny tests. It has been discussed because it introduces the subject of progeny tests in an uncomplicated fashion.

Incomplete dominance of one gene pair. When one of the gene pairs is dominant and the other incompletely dominant, there are three phenotypic classes that include more than a single genotype, namely, A_BB, A_Bb, and A_bb. Of these classes the first and third provide information about linkage only in connection with the completion of the classification of the F_2. This being the case, progeny tests have only to distinguish between the genotypes AA and Aa. Misclassification can occur only if the progeny of Aa F_2 plants fail to include a recessive individual. Assurance against this $(P = 0.99)$ will be obtained if each progeny contains at least 16 plants.[3]

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[3] The number of individuals, n, required for a given type to occur at least once with a probability P is given by $n = \dfrac{\log (1 - P)}{\log (1 - X)}$, where X is the fraction of the progeny expected to be of the type in question.

The amount of information (i_p) obtained from each A—bb progeny classified is given by $2/p(1 - p)(1 + p)^2$ and from each A—bb progeny by $2/p(1 - p)(2 - p)^2$. The information provided by a single F_2 plant can be obtained from table 8. Since each progeny requires that 16 plants be raised, the ratio of the two values (i_pF_3/i_pF_2) must exceed 16 if progeny tests are to be profitable. Neither ratio approaches the required magnitude even in close repulsion where they reach their largest values. It may therefore be concluded that progeny tests of the A—BB and A—bb phenotypes have no place unless special circumstances are involved.

The remaining phenotype A—Bb includes three genotypes, AB/Ab, AB/ab, and Ab/aB. In progeny tests it is capable of providing two sorts of information, that obtained by completing the classification of the F_2 and further F_2 information supplied by the progeny of both coupling and repulsion doubly heterozygous F_2 plants. Misclassification can result from two causes: failure of Aa heterozygotes to produce a recessive and inability to separate coupling from repulsion heterozygotes. Rearing 16 plants will provide an accuracy of 99/100 as regards the first cause of difficulty. The size of progeny required to separate AB/ab from Ab/aB can be determined by Immer's method. It turns out that 14 plants are required at $p = 0.20$ and 46 plants at $p = 0.30$. The first possible cause for misclassification thus dictates larger progenies than the second cause at values of $p \leq 0.21$.

If progeny tests of the A—Bb phenotype are to be profitable, the amount of information obtained from each progeny classified, plus the additional F_2 type of information from the segregation of AB/ab and Ab/aB plants, must exceed the information obtained from raising additional F_2's, taking account of the fact that each F_3 line need contain several individuals.

Each A—Bb individual classified contributes $1 + 2p - 2p^2/p(1 - p)(1 - p + p^2)^2$ units of information. In addition, the doubly heterozygous families contribute F_2 type of information. The amount of this information may be calculated as the product of the i_p value in table 8 multiplied by the expected frequency of the type of family, that is, $(1 - p)^2/2(1 - p + p^2)$ and $p^2/2(1 - p + p^2)$ for coupling and repulsion respectively. The sum of these two sorts of information fails to reach a value 16 times as large as the value of i_p for the F_2. Hence the progeny tests of the A—Bb phenotype are also not profitable under ordinary circumstances.

Both gene pairs completely dominant. Up to this point progeny tests, with one exception, have not been profitable as compared with the raising of additional F_2 individuals. This is readily understood when it is realized: (*a*) that each F_3 line must contribute at least 16 times as much information as an F_2 individual, and (*b*) that the F_2 segregations considered to this point have been those giving comparatively large i_p values. When both gene pairs are completely dominant, the number of recognizable classes in F_2 is reduced to four, with the result that i_p values are small, particularly in close repulsion. It might therefore be expected that progeny tests will be more valuable here than raising additional F_2 individuals. There are three phenotypic classes that include more than one genotype—the two singly dominant classes A—bb and aaB— and the doubly dominant class A—B—. Immer (1934) and Mather (1936) have considered progeny tests of both the singly and doubly dominant classes and have found that progeny tests are profitable for certain

values of p. Mather's calculations were based upon raising large enough progenies for accurate identification in 999 cases out of 1,000. Immer proposed progenies of 25 plants, thus providing slightly greater accuracy of classification than Mather for singly dominant progenies but generally less accuracy for the doubly heterozygous progenies. The following calculations maintain the odds of 99:1 used elsewhere in this paper.

Consideration will be given first to the two singly dominant classes, which are equally useful in estimating linkage. Using the methods of the previous section, the calculations reveal that F_3 progenies of 16 plants provide more information than F_2's when $p < 0.11$ in repulsion. When the accuracy is increased to 0.999, requiring 24 plants per progeny, progeny testing is profitable up to $p = 0.08$ (Mather, 1936).

Progeny tests of doubly dominant F_2 plants can provide both information from completing the classification of the original F_2 and the F_2 type of information yielded by the double heterozygotes. Only the former type of information is obtained where it is desired or possible to classify doubly dominant individuals into homozygotes, single heterozygotes, and double heterozygotes, ignoring the separation of double heterozygotes as to linkage phase. The amount of information thus obtained per line in close repulsion is practically identical to that obtained from singly dominant lines (table 8, formulas 12 and 14). However, classification is slightly more difficult with the doubly dominant progenies, requiring 18 plants per progeny to assure ($P = 0.99$) detection of segregation for both gene pairs in double heterozygotes. Hence, of these two types of progeny tests, the one with singly dominant F_2 individuals is preferred.

If the double heterozygotes are identified as to linkage phase, the completeness of the classification of the original F_2 is increased (compare formulas 13 and 14), and the F_2 type of information from the double heterozygotes also becomes available. Hence this separation will make possible a more efficient progeny test than the previous types if it can be accomplished with progenies of reasonable size. The minimum number of progeny must first of all be sufficiently large so that no more than one family per 100 will fail to show segregation for both gene pairs. This requires 18 individuals per progeny. Secondly, progeny sizes must permit separation of double heterozygotes into the AB/ab and Ab/aB genotypes. This requires 18 plants at $p = 0.10$, 37 plants at $p = 0.20$, and 89 plants at $p = 0.30$. Up to $p = 0.10$ the number of plants per progeny is determined by the first consideration and need be only 18. With looser linkage the second requirement becomes the more stringent, and the number of plants per progeny must be increased accordingly. The maximum value of p for which progeny tests are profitable is the point at which the ratio of the F_3 to F_2 information is equal to the number of plants required for accurate classification. This occurs between $p = 0.13$ and 0.14.

The policy with regard to the use of F_3 families may be summarized as follows. Doubly dominant F_3 families completely classified are the preferred source of information. They can be grown more profitably than additional F_2 individuals up to $p = 0.14$ in repulsion. Singly dominant families are to be preferred to doubly dominant ones classified only into homozygotes and single and double heterozygotes, since they provide nearly as much information per family and there is less chance for error in the classification of the single

dominants. At values larger than $p = 0.11$ in repulsion additional F_2 individuals are more efficient than either of these latter two progeny tests unless special circumstances are involved.

Burnham and Kramer (1947) have given a numerical example of the combination of F_2 and F_3 data of this type in the estimation of linkage.

Progeny tests from the 9:6:1 F_2 ratio. This case is identical to the previous one and provides one example where less complete classification does not lead to a loss of information.

Progeny tests from the 12:3:1 F_2 ratio. Here only one of the singly dominant phenotypes, aaB__, is useful in estimating linkage. This phenotype includes two genotypes, aB/aB and aB/ab, whose separation depends only upon the appearance of at least one aabb individual in progenies derived from aaBb. As seen earlier, this can be accomplished 99 times in 100 if each progeny contains 16 individuals. Since each progeny provides $2/p(1 + p)$ $(1 - p^2)$ units of information and each F_2 individual $1/1 - p^2$ units of information, progeny tests will be profitable when the ratio of the former to the latter expression exceeds 16. The ratio is very large with tight linkage in repulsion, so progeny tests are very much worthwhile under those circumstances. At $p = 0.11$ in repulsion, F_2 and F_3 data become equally valuable. Progeny tests will not ordinarily be advantageous if p exceeds 0.11.

Progeny tests of F_2 plants phenotypically AB present difficulties in identifying one or more genotypes regardless of the value of p. With very tight linkage in repulsion (up to $p \approx 0.05$) fairly certain classification of the F_3 progenies into one homozygous and two heterozygous classes is possible with small progenies. However, each of these progenies gives less information than may be had from progenies derived from aaB__ plants. With looser linkage, the progeny sizes required for the identification of several of the genotypes become large, and the information per progeny is not greatly different from that obtained from progeny tests of the single heterozygote. Therefore, only under most unusual circumstances should progeny tests of AB plants be attempted.

Progeny tests from the 9:3:4 ratio. Only two of the F_2 phenotypes, A__B__ and aaB__, supply information on linkage. The situation with respect to the aB phenotype is exactly parallel to the case of this phenotype in the 12:3:1 ratio. Since, however, the F_2 is less efficient in the present situation, it might be expected that progeny testing would be profitable over a wider range of p values. It turns out that the threshold value of p is 0.40. Hence, progeny tests of the aaB__ phenotype are at least equally valuable with the F_2 on a plant-to-plant basis up to this comparatively high p value. At low values of p the progeny tests are tremendously more efficient than the F_2.

The A__B__ phenotype contains five genotypes and hence is capable of providing considerable information about linkage with complete classification. First, consider the separation of the double heterozygotes as to linkage phase. The number of plants required for this separation will be $(P = 0.99)$:

$$n = \left[\frac{2.58 \left(\sqrt{\dfrac{(1 - p^2)(2 + p^2)}{3p^2}} + \sqrt{\dfrac{(1 - q^2)(2 + q^2)}{3q^2}} \right)}{q - p} \right]^2 .$$

This function of p reaches a minimum at $p = 0.21$ so that larger numbers of plants are required at higher or lower values of p. Since 411 plants are required at $p = 0.21$, the futility of attempting this separation is obvious.

While inability to separate the double heterozygotes as to linkage phase lessens the attractiveness of progeny tests of the A_B_ phenotype, it does not eliminate such progeny tests from consideration. Unfortunately, the genotypes AB/ab and AB/Ab are also separated with difficulty. The AB/ab

genotype produces a ratio of $\dfrac{3 - 2p + p^2}{4} A\_B\_ : \dfrac{2p - p^2}{4} A\_bb : \frac{1}{4} aabb$

so that A_bb individuals are quite infrequent if p is small. If the AB/ab genotype is to be separated from AB/Ab, sufficiently large progenies must be grown to guarantee with reasonable probability the occurrence of at least one Abb individual. Such individuals make up 16 per cent of each family at $p = 0.40$, 12.75 per cent at $p = 0.30$, 9 per cent at $p = 0.20$, and 4.75 per cent at $p = 0.10$. Thus, if the appearance of at least one A_bb individual is to be assured in the progeny of each double heterozygote, 26, 34, 40, and 95 individuals, respectively, are required per family as p varies from 0.40 to 0.30 to 0.20 and to 0.10. The usefulness of this type of progeny test will therefore depend upon the amount of information it gives relative to the F_2 and to progeny tests of the aaB_ phenotype.

Regardless of the value of p, progeny tests of singly vs. doubly dominant individuals are not strikingly different in the amounts of information they give. The double dominant gives slightly more information than the single dominant from $p = 0.00$ to $p = 0.18$, and from $p = 0.69$ to $p = 0.99$. The reverse is true for the remaining values of p. Thus, in the range of $p = 0.00$ to $p = 0.18$ in repulsion the singly dominant phenotype is the best source of linkage information because it gives very nearly as much information per progeny as the double dominant, and it can be classified into genotypes with smaller populations. From $p = 0.18$ to $p = 0.40$ the single dominants are even more advantageous because, in addition to the advantage of easier classification, the i_p values are larger. When $p > 0.40$ the F_2 provides more information per plant than progeny tests and is therefore to be recommended. These results therefore indicate that progeny tests of doubly dominant individuals have no place in the measurement of linkage from the 9:3:4 ratio. These conclusions are different from those of Immer (1934).

Progeny tests from the 13:3 F_2 ratio. Because of the low efficiency of this segregation throughout most of its range (table 8), F_3 progeny tests might be expected to be useful. For each progeny phenotypically aaB separated into the genotypes aB/aB and aB/ab, $2 p(1 + p) (1 - p^2)$ units of information are obtained contrasted to $4p^2/(3 + p^2) (1 - p^2)$ units per F_2 individual. The separation of aB/aB and aB/ab can be made with 16 individuals. Progeny tests are therefore extremely valuable in close repulsion, become equally valuable with the F_2 on a plant-for-plant basis at $p = 0.41$, and provide less information per plant at higher values of p.

Progeny tests of the A_ (or ab) phenotype are complicated by difficulties of classification. In the first place, separation of the double heterozygotes as to linkage phase requires impractically large populations. Second, the AB/ab

genotype is difficult to separate from homozygous AB/AB at low p values, since the former produces only $\dfrac{p(2-p)}{4}$ aaB_ individuals. Two dispositions of this genotype are possible: (a) with low values of p it could be included with lines homozygous for the A_ phenotype; (b) with looser linkage it could be included with those genotypes producing 3A_:1aB. Under situation (a) the estimation equation is

$$\frac{dL}{dp} = (e + f + h + j + k + n)\left(\frac{2}{1+p}\right) + (g + i)\left(\frac{-1}{1-p}\right)$$

$$+ \ m\left(\frac{1-2p}{p(1-p)}\right) + l\left(\frac{-2}{1-p}\right) = 0 ,$$

and the amount of information per family classified is

$$i_p = \frac{p+1}{2p(1-p)}.$$

In situation (b) the estimation equation is

$$\frac{dL}{dp} = (e + f + j + h + n)\left(\frac{2-2p}{1+2p-p^2}\right) + (g + h + i)\left(\frac{2p-1}{1-p+p^2}\right)$$

$$+ \ m\left(\frac{1-2p}{p-p^2}\right) + l\left(\frac{-2}{1-p}\right) = 0 ,$$

and the i_p value is given by

$$1 + \frac{(1-p)^2}{1+2p-p^2} + \frac{(1-2p)^2}{2(1-p+p^2)} + \frac{(1-2p)^2}{2p(1-p)} .$$

Progeny tests from the 15:1 F$_2$ ratio. The ratio (A_:ab) occurring within F$_3$ progenies will be one of the following four types: 1:0, 3:1, $3 + 2p - p^2 : 1 - 2p + 2p^2$, or $4 - p^2 : p^2$. The first two categories are, of course, easily distinguished from one another, only 16 plants being required per progeny. However, separating the final two segregations, which result from the coupling and repulsion double heterozygotes respectively, from each other and from the other types is more difficult. Because of the low efficiency of the F$_2$ type of data and the correspondingly high standard errors, separation of AB/ab and Ab/aB as to linkage phase is impractical regardless of the value of p. Also the repulsion-phase double heterozygote produces only 6.25 per cent of ab phenotypes at $p = 0.50$ and even fewer with lower values of p. It therefore appears hopeless to attempt to separate this segregation from the 1:0 type since 71 individuals per family would be required with independence and greater numbers with linkage. At $p = 0.50$ these families could be distinguished 19 times out of 20 from families segregating 3:1 with progenies of 35 individuals, although 82 per family would be required if the probability is set at 0.99. The numbers required become increasingly smaller with closer

linkage. With close linkage there appears to be little likelihood for misclassification if the $\frac{Ab}{aB}$ genotype is classified with 1:0 families, that is, families homozygous for the A— phenotype.

The classification of the coupling double heterozygote is also troublesome in that the expected number of ab individuals changes from 25 per cent to 6.25 per cent as p changes from 0.00 to 0.50. With close linkage these double heterozygotes can probably be included with the single dominants without danger of confusion.

The following procedures can therefore be recommended for progeny tests. The identification of only three types of families should be attempted. With tight linkage, the estimation equation is

$$\frac{dL}{dp} = (e + f + g + j + l + i)\,\frac{2}{p - 2}$$

$$+ (k + m + h)\left[\frac{2(1 - p)}{p(2 - p)}\right] + n\left(\frac{2}{p}\right) = 0 \;,$$

and each family provides $\dfrac{2(1 - 3p)}{p(2 - p)^2}$ units of information. If the minimal family size is arbitrarily set at 35 individuals, such progeny tests are profitable compared with the F_2 at p values up to 0.03 in repulsion.

If the linkage is loose, not only the coupling but repulsion double heterozygotes should be classified with 3:1 families. The estimation equation then becomes

$$\frac{dL}{dp} = (e + f + g + j + l)\left(\frac{2p}{2 - p^2}\right) + n\left(\frac{-2}{p}\right) = 0$$

and each family provides $2/2 - p^2$ units of information. This sort of progeny test would, of course, be useful only if classification on a single-plant basis is difficult and progeny tests are essential for the identification of genotypes.

Progeny tests with complementary genes. Since this F_2 has the lowest efficiency of any commonly encountered, it might be surmised that progeny tests would be extremely valuable here. The single dominants obviously provide no information about linkage, so progeny tests are necessarily confined to the AB phenotype. In this phenotype are included genotypes producing one of the following four ratios (AB:Ab, aB, or ab): 1:0, 3:1, $3 - 2p + p^2$: $1 + 2p - p^2$, or $2 + p^2 : 2 - p^2$.

Separating the first two categories is easy. However, much difficulty is associated with the separation of the coupling and repulsion double heterozygotes from each other and from the first two groups. The same procedure used previously shows that it is idle to contemplate separating double heterozygotes as to linkage phase, the progeny sizes required being very large. Difficulty is also encountered in separating the second and third ratios. The ratio $3 - 2p + p^2$: $1 + 2p - p^2$ has a value of 9:7 when $p = 0.50$. Such progenies must contain at least 133 individuals if they are to be distinguished from the 3:1 ratio. With linkage, larger progenies are needed. In the fourth category the ratio changes from 9:7 to 1:1 as p changes from 0.50 to 0.00.

To distinguish between 3:1 and 1:1 ratios requires 113 plants. In other words, the only separation easily made is into homozygous lines vs. segregating lines. The appropriate estimation equation is therefore

$$\frac{dL}{dp} = e\left(\frac{2}{p}\right) - (e + f + g + h + i)\left(\frac{2p}{2 + p^2}\right) = 0 \ .$$

This separation provides $\dfrac{4(1+2p^2)}{(2+p^2)^3}$ units of information per family, and

since it can be made with 16 plants, progeny tests will be useful so long as the ratio

$$\frac{4(1 + 2p^2)}{(2 + p^2)^3} : \frac{4p^2}{(2 + p^2)(2 - p^2)}$$

exceeds 16. Therefore, progeny tests are useful over the range $p = 0.00$ to $p = 0.18$.

Estimating Linkage from Incomplete F_2 Ratios

In the segregations considered up to this point, the assumption was made that all of the genotypes were viable. In practice, F_2 ratios are frequently encountered in which certain genotypes are either inviable or effectively inviable in that they cannot be accurately classified, or for some practical reason are difficult to handle. Several ratios of this type will now be considered from the standpoint of their value in the measurement of linkage.

In one of the more common of these situations linkage is measured from the ratio produced within one of the recessive classes. Seed-coat color and indeterminate habit of growth (vine) in lima beans are an example. Vine individuals (D_) of certain hybrids mature so late that they usually fail to set seeds in the field. This, coupled with their large space requirement, makes it more efficient to rogue them as soon as they can be recognized early in growth and to classify only bush plants for seed-coat color. This procedure will be recognized as equivalent for the purpose of estimating linkage to the 12:3:1 ratio (equation 7). This type of progeny is quite efficient with close coupling and reasonably efficient in the repulsion range (table 8 and figure 2). If the heterozygote can be identified because of incomplete dominance, that is, the aB/aB, aB/ab, and ab/ab genotypes are all recognizable, the efficiency is considerably increased in repulsion and also through nearly all of the coupling range. Thus, if dominance is complete, progeny tests to separate genotypes aB/aB and aB/ab may be justified. Since each F_2 individual contributes $1/1 - p^2$ units and each F_3 line $1/p(2 - p)$ units of information, progeny tests will be profitable when $p < 0.03$ in repulsion.

A parallel situation exists when linkage is measured from the segregation within one of the dominant classes. This procedure is equivalent to estimation from the 9:3:4 ratio and the appropriate equation is number 9.

Three types of ratios encountered fairly frequently result from combinations of F_2 and F_3 data. The most common is the 3:1/2:1, producing a ratio of 6:3:2:1 when $p = 0.50$. This is an extension of the ratio of 3:1 within the dominant class, since it involves classification of the other gene

pair into a 2:1 ratio. An example is provided by the classification into a 3:1 ratio in the field for an adult plant character followed by classification into a 2:1 ratio in the greenhouse for a seedling lethal. The estimation equation is number 18.

If the heterozygotes are identified either as a result of incomplete dominance or progeny tests, the result is a 1:2:1 ratio superimposed on a 2:1, or a ratio of 2:4:2:1:2:1 when $p = 0.50$. The estimation equation is number 19.

The third ratio of this type is the 2:1/2:1. Although not common, this situation has been encountered when both recessives were so weak that survival was very poor under field conditions and a progeny test in the greenhouse was required for the measurement of linkage. This will be recognized as equivalent to testing A_B_ phenotypes in the 3:1/3:1 situation. The appropriate estimation equations are therefore numbers 13 or 14, depending upon circumstances.

Another type of case leading to a 2:1/2:1 ratio has been encountered by Dr. C. M. Rick with characters in tomatoes such as wooly (Wo) and Xantha (Xa). With either gene homozygous dominant individuals die, with the result that the F_2 estimation equation takes the form

$$\frac{dL}{dp} = (h + i) \frac{2(2p - 1)}{1 - 2p + 2p^2} + (k + m) \frac{1 - 2p}{p(1 - p)} + n \left(\frac{2}{p}\right)$$
$$- (h + i + k + m + n) \left(\frac{2p}{2 + p^2}\right) = 0 ,$$
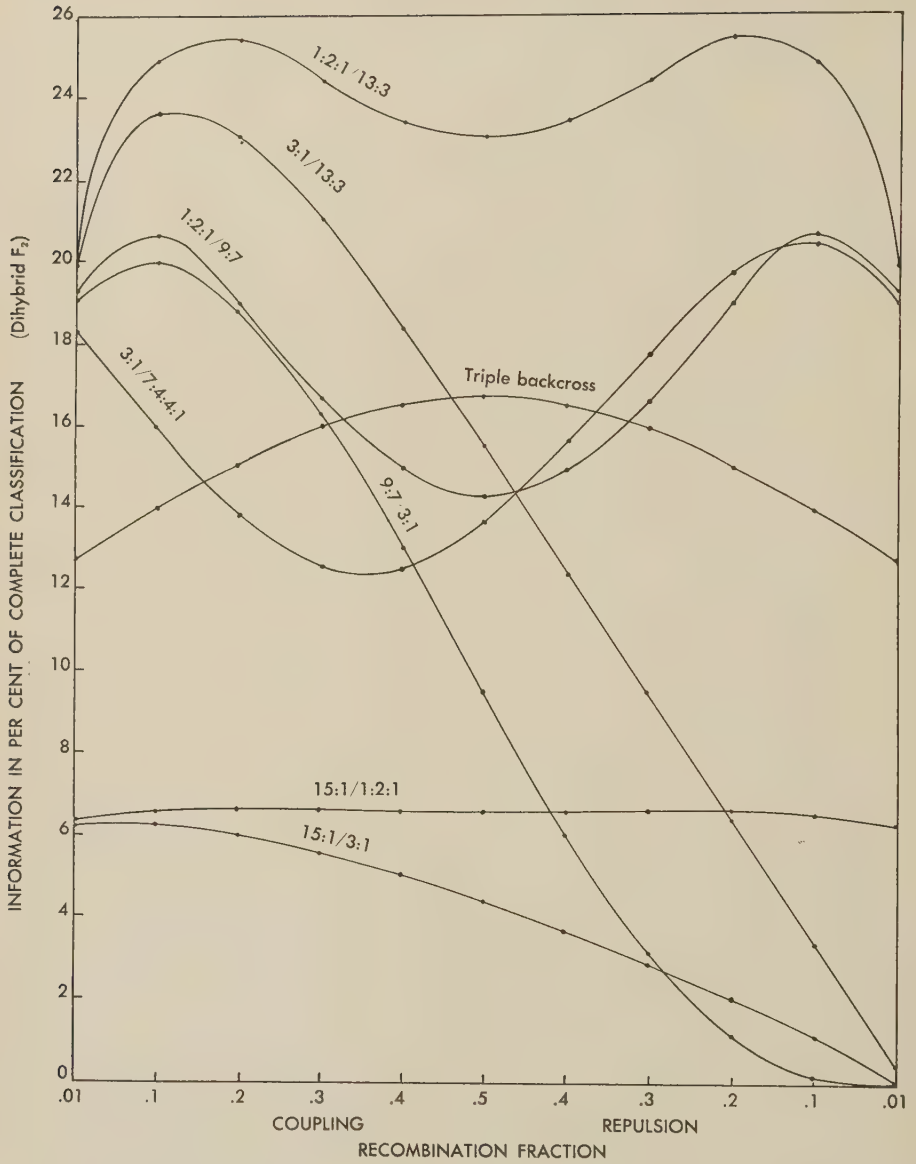
and the i_p value is

$$\frac{1 - 3p + p^2 + 4p^3 - 2p^4}{p(1 - p)(1 - 2p + 2p^2)} .$$

Measurement of Linkage when a Gene is Linked with a Member of a Complementary or Duplicate Pair or a Pair Producing a 13:3 Ratio

Hutchinson (1929) has considered the problem of estimating linkage values when one member of a complementary or duplicate pair is linked to a third gene pair. His results indicated that F_2 data are very low in efficiency so that large populations are required to obtain reliable measurements of recombination values. The present extension is intended to point out some ways of increasing the efficiency of estimation.

In general, two procedures are available to the investigator confronted by data of this sort: he can raise the progenies to identify the double heterozygotes suitable for estimating linkage by equation 6, or he can progeny-test the F_2 families available to him. Only the second case need be considered here. Symbols for observed and expected numbers in various distinguishable classes are given in table 5. Estimation equations and i_p values are given in tables 6 and 8 respectively.

Linkage with a member of a complementary pair. It is apparent from table 8 and figure 3 that the 9:7/3:1 F_2 segregation is quite uninformative about linkage, particularly in close repulsion. It can also be seen that the identification of AA and Aa greatly increases the amount of information

INFORMATION IN PER CENT OF COMPLETE CLASSIFICATION (Dihybrid F₂)

RECOMBINATION FRACTION

COUPLING   REPULSION

1:2:1/13:3

3:1/13:3

1:2:1/9:7

3:1/7:4:4:1

Triple backcross

9:7/3:1

15:1/1:2:1

15:1/3:1

in the repulsion range. An investigation of the comparative efficiency of F_2 and F_3 shows that progeny tests will be profitable in the range $p = 0.00$ to 0.21 in repulsion.

Linkage with a member of a duplicate pair. The $15:1/3:1$ F_2 segregation also contributes little information about linkage (table 8 and figure 3). Identification of AA and Aa leads to increases in the amount of information, particularly in close repulsion. By methods used previously it can be shown that this progeny test is profitable only in repulsion in the range $p = 0.00$ to 0.03.

Progeny tests also make it possible to separate individuals phenotypically B_C_ into two nonsegregating and two segregating classes, $3:1$ and $15:1$. This separation requires 82 individuals if the probability is set at 0.99. From table 8 it is easily determined that this separation is profitable only in extremely tight repulsion. If the separation of AA and Aa is also made, 12 classes are identified and the amount of information is substantially increased. This separation requires only 16 individuals which may be in addition to the 82 individuals required for the above separations, if, for example, both a seedling and an adult plant character are involved. Compared to the $15:1/3:1$ segregation in F_2, this progeny test is profitable in repulsion up to $p = 0.03$ or 0.04, according to the requirement of 82 or 98 individuals per progeny.

Linkage with a gene pair producing a 13:3 ratio. The $13:3/3:1$ segregation in F_2 also has low efficiency in close repulsion. By methods used previously it can be shown that progeny tests to separate AA and Aa are profitable for the range $p = 0.00–0.04$ in repulsion.

SUMMARY

In estimating recombination values in heredity, several types of genetic data are frequently available. For example, backcross, F_2, and F_3 data from both coupling and repulsion crosses might exist. When complex data are encountered, a single joint estimate of the recombination value which best fits all the data can be made with the method of maximum likelihood. Further, the homogeneity of the data can be examined with little additional computation. Estimation equations are given for various backcross, F_2, and F_3 situations, including equations for estimating linkage intensities between a member of a complementary or duplicate pair, or a gene pair producing a 13:3 ratio, and a third gene pair. Tables of scores to facilitate the numerical solution of these equations are included. Also provided are tables to facilitate the calculation of the standard errors of the recombination values.

Tremendous variations in the value of various sorts of genetic data for the estimation of recombination fractions make advance planning an important feature of linkage investigations. In this regard the value of different sorts of genetic data is examined for a variety of situations under the assumption that positive classification of single plants is possible. The results of this evaluation can easily be adapted to situations where classification of single plants is not positive and progeny tests are a necessary feature of inheritance studies, as for example in studies of the inheritance of resistance to many diseases.

ACKNOWLEDGMENT

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TABLE 1

F$_2$ AND F$_3$ DATA FROM LIMA BEAN HYBRIDS SEGREGATING FOR THE
GENE PAIRS Dd AND Rr

</div>

Data set no.	Type of data	Observed frequencies of phenotype and genotype*												
		a	b	c	d	e	f	g	$h+i$	j	k	l	m	n
1	F$_2$ coupling......	200	57	49	30	..	..	..	..	..	..	..	..	..
2	F$_2$ coupling......	842	234	255	126	..	..	..	..	..	..	..	..	..
3	F$_2$ coupling......	274	71	64	45	..	..	..	..	..	..	..	..	..
4	F$_2$ repulsion......	293	107	119	35	..	..	..	..	..	..	..	..	..
5	F$_2$ repulsion.....	50	21	30	0	....	..	..	..	..	..	..	..	..
6	1 : 2 : 1 within recessive class....	..	..	..	..	..	..	..	..	..	..	8	28	36
7	2 : 1/1 : 2 : 1......	..	..	..	..	7	13	14	31	2	10	..	..	..
8	3 : 1/1 : 2 : 1......	..	..	..	..	16	..	43	..	27	..	5	16	12
9	1 : 2 : 1 within dominant class.	..	..	..	..	20	..	46	..	11	..	..	..	..

* See table 4 for significance of symbols.

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TABLE 2

ESTIMATION OF THE RECOMBINATION VALUE FROM THE DATA OF
TABLE 1 AND THE EXAMINATION FOR HETEROGENEITY,
USING FISHER'S SCORING METHOD

</div>

Data set no.	Estimation equation no.	$p = 0.50$		$p = 0.39$		$p = 0.40$		χ^2
		Score	Information	Score	Information	Score	Information	
1..............	6	−67.5555502	597.408	4.7332726	786.912	−2.9449190	765.408	0.011
2..............	6	−226.2222011	2590.546	103.9538460	3412.294	68.7393910	3319.046	1.424
3..............	6	−121.7777701	807.212	−26.1596043	1063.268	−36.1970389	1034.212	1.267
4..............	6	−31.1111166	985.012	77.7792568	791.666	68.2804212	806.070	5.783
5..............	6	−45.7777783	179.578	−28.7940748	144.329	−30.0529110	146.955	6.146
6..............	16	−112.0000000	144.000	−51.1139128	151.344	−56.6666664	149.976	21.411
7..............	19	−20.0000000	154.000	−4.4989555	191.730	−6.3461558	185.108	0.218
8..............	5	−13.3333337	317.373	26.4216957	345.695	22.4044475	340.697	1.473
9..............	17	−11.9999997	51.359	−10.3046614	61.908	−10.5278834	59.983	1.848
		−649.7777497	5826.488	92.0168623	6949.146	16.6886852	6807.455	39.581

$$\frac{-649.778}{5826.488} = -0.112$$

$$\frac{92.017}{6949.146} = 0.0132$$

$$\frac{16.689}{6807.455} = 0.0025$$

$p = 0.50 - 0.11 = 0.39$ $p = 0.39 + 0.01 = 0.40$ $p = 0.400 + 0.0025 = 0.4025$

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TABLE 3

RECOMBINATION VALUES AND STANDARD
ERRORS FOR THE NINE SETS OF
DATA OF TABLE 2

</div>

Data set	Recombination value (p), per cent
1	39 ± 3.6
2	42 ± 1.8
3	36 ± 2.9
4	47 ± 3.3
5	0.0 ± 10.0
6	31 ± 7.7
7	36 ± 6.8
8	46 ± 5.6
9	24 ± 9.0

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TABLE 4

SYMBOLS FOR OBSERVED AND EXPECTED FREQUENCIES OF VARIOUS
GENOTYPES AND PHENOTYPES OCCURRING AMONG THE
SELFED PROGENY OF AaBb INDIVIDUALS

</div>

Phenotype or genotype	Observed frequency	Expected frequency in F_2*	
		Coupling	Repulsion
A__B__	a	$\frac{1}{4}(3 - 2p + p^2)$	$\frac{1}{4}(2 + p^2)$
A__bb	b	$\frac{1}{4}(2p - p^2)$	$\frac{1}{4}(1 - p^2)$
aaB__	c	$\frac{1}{4}(2p - p^2)$	$\frac{1}{4}(1 - p^2)$
aabb	d	$\frac{1}{4}(1 - p)^2$	$\frac{1}{4}p^2$
$\frac{AB}{AB}$	e	$\frac{1}{4}(1 - p)^2$	$\frac{1}{4}p^2$
$\frac{AB}{aB}$	f	$\frac{1}{2}p(1 - p)$	$\frac{1}{2}p(1 - p)$
$\frac{AB}{Ab}$	g	$\frac{1}{2}p(1 - p)$	$\frac{1}{2}p(1 - p)$
$\frac{AB}{ab}$	h	$\frac{1}{2}(1 - p)^2$	$\frac{1}{2}p^2$
$\frac{Ab}{aB}$	i	$\frac{1}{2}p^2$	$\frac{1}{2}(1 - p)^2$
$\frac{Ab}{Ab}$	j	$\frac{1}{4}p^2$	$\frac{1}{4}(1 - p)^2$
$\frac{Ab}{ab}$	k	$\frac{1}{2}p(1 - p)$	$\frac{1}{2}p(1 - p)$
$\frac{aB}{aB}$	l	$\frac{1}{4}p^2$	$\frac{1}{4}(1 - p)^2$
$\frac{aB}{ab}$	m	$\frac{1}{2}p(1 - p)$	$\frac{1}{2}p(1 - p)$
$\frac{ab}{ab}$	n	$\frac{1}{4}(1 - p)^2$	$\frac{1}{4}p^2$

* Backcross repulsion phase expectancies for the AB and ab and the Ab and aB phenotypes are $\frac{1}{2}p$ and $\frac{1}{2}(1 - p)$ respectively.

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Table 5

SYMBOLS FOR OBSERVED AND EXPECTED FREQUENCIES OF VARIOUS
GENOTYPES AND PHENOTYPES WHEN TWO CHARACTERISTICS
ARE GOVERNED BY THREE GENE PAIRS.

The Symbols Bb and Cc represent the epistatic gene pairs in each case.

</div>

Backcross to triple recessive

Phenotype	Frequency	
	Observed	Expected
A__B__C__	o	$\frac{1}{4}p$
A__B__cc	q	$\frac{1}{4}p$
A__bbC__	r	$\frac{1}{4}(1-p)$
A__bbcc	s	$\frac{1}{4}(1-p)$
aaB__C__	t	$\frac{1}{4}(1-p)$
aaB__cc	u	$\frac{1}{4}(1-p)$
aabbC__	v	$\frac{1}{4}p$
aabbcc	w	$\frac{1}{4}p$

Complementary pair

Phenotype	Frequency	
	Observed	Expected
AABC	a'	$1/8(3p-p^2)$
AaBC	b'	$3/8(1-p+p^2)$
aaBC	c'	$3/16(1-p^2)$
AABc(bC,bc)	d'	$1/16(4-6p+3p^2)$
AaBc(bC,bc)	e'	$1/8(1+3p-3p^2)$
aaBc(bC,bc)	f'	$1/16(1+3p^2)$

Duplicate pair

Phenotype	Frequency	
	Observed	Expected
AABB___(___CC)	g'	$1/16(1+3p^2)$
AaBB___(___CC)	h'	$1/8(1+3p-3p^2)$
aaBB___(___CC)	i'	$1/16(4-6p+3p^2)$
AABbCc	j'	$1/4p(1-p)$
AaBbCc	k'	$1/4(1-2p+2p^2)$
aaBbCc	l'	$1/4p(1-p)$
AABbcc	m'	$1/8(1-p)$
AaBbcc	n'	$1/8$
aaBbcc	o'	$1/8p$
AAbbcc	q'	$1/16(1-p)^2$
Aabbcc	r'	$1/8p(1-p)$
aabbcc	s'	$1/16p^2$

Gene pair producing 13 : 3

Phenotype	Frequency	
	Observed	Expected
AABC(Bcc,bbcc)	t'	$1/16(1+6p-3p^2)$
AaBc(Bcc,bbcc)	u'	$1/8(4-3p+3p^2)$
aaBC(Bcc,bbcc)	v'	$1/16(4-3p^2)$
AAbbC	w'	$3/16(1-p)^2$
AabbC	x'	$3/8p(1-p)$
aabbC	y'	$3/16p^2$

Table 6

SUMMARY OF MAXIMUM LIKELIHOOD EQUATIONS FOR DETERMINING RECOMBINATION VALUES FROM DIFFERENT TYPES OF BACKCROSS, F₂ AND F₃ DATA IN REPULSION PHASE AND FORMULAS FOR CALCULATING THE MEAN AMOUNT OF INFORMATION CONTRIBUTED PER F₂ INDIVIDUAL OR F₃ FAMILY. COUPLING PHRASE EQUATIONS CAN BE OBTAINED BY SUBSTITUTING $1-p$ FOR p ACCOMPANIED BY A SIGN REVERSAL. (SEE TEXT.)

Equation or formula	Type of data*	Estimation equation	Information (i_p)
1	F₂ Complete classification	$(e+h+n)\left(\dfrac{2}{p}\right) + (f+g+k+m)\left[\dfrac{1-2p}{p(1-p)}\right] + (i+j+l)\left(\dfrac{2}{p-1}\right) = 0$	$\dfrac{2}{p(1-p)}$
2	Backcross 1:1:1:1	$(a+d)\left(\dfrac{1}{p}\right) + (b+c)\left(\dfrac{1}{p-1}\right) = 0$	$\dfrac{1}{p(1-p)}$
3	Backcross 3:1†	$a\left(\dfrac{1}{p}\right) + (b+c+d)\left(\dfrac{1}{p-2}\right) = 0$	$\dfrac{1}{p(2-p)}$
4	F₂ 1:2:1:2:4:2:1:2:1	$(e+n)\left(\dfrac{2}{p}\right) + (f+g+k+m)\left[\dfrac{1-2p}{p(1-p)}\right] + (j+l)\left(\dfrac{2}{p-1}\right) + (h+v)\left[\dfrac{2(2p-1)}{1-2p+2p^2}\right] = 0$	$\dfrac{2(1-3p+3p^2)}{p(1-p)(1-2p+2p^2)}$
5	F₂ 3:6:3:1:2:1	$(e+f)\left(\dfrac{2-2p}{2p-p^2}\right) + (g+h+v)\left(\dfrac{2p-1}{1-p+p^2}\right) + (j+k)\left(\dfrac{-2p}{1-p^2}\right) + l\left(\dfrac{2}{p-1}\right) + m\left(\dfrac{1-2p}{p-p^2}\right) + n\left(\dfrac{2}{p}\right) = 0$	$2 + \dfrac{(1-p)^2}{p(2-p)} + \dfrac{(1-2p)^2}{2(1-p+p^2)} + \dfrac{p^2}{1-p^2} + \dfrac{(1-2p)^2}{2p(1-p)}$
6	F₂ 9:3:3:1†	$a\left(\dfrac{2p}{2+p^2}\right) + (b+c)\left(\dfrac{-2p}{1-p^2}\right) + d\left(\dfrac{2}{p}\right) = 0$	$\dfrac{2(1+2p^2)}{(2+p^2)(1-p^2)}$
7	F₂ 12:3:1	$c\left(\dfrac{-2p}{1-p^2}\right) + d\left(\dfrac{2}{p}\right) = 0$	$\dfrac{1}{1-p^2}$
8	F₂ 13:3	$(a+b+d)\left(\dfrac{2p}{3+p^2}\right) + c\left(\dfrac{-2p}{1-p^2}\right) = 0$	$\dfrac{4p^2}{(3+p^2)(1-p^2)}$
9	F₂ 9:3:4	$a\left(\dfrac{2p}{\ldots}\right) + b\left(\dfrac{-2p}{\ldots}\right) = 0$	$\dfrac{2p^2}{\ldots}$

		Equation	Result
11	F₂ 9:7	$a\left(\dfrac{2p}{2+p^2}\right) + (b+c+d)\left(\dfrac{-2p}{2-p^2}\right) = 0$	$\dfrac{4p^2}{(2+p^2)(2-p^2)}$
12	F₃ from singly dominant F₂§	$j\left(\dfrac{2}{p-1}\right) + k\left[\dfrac{1-2p}{p(1-p)}\right] - (j+k)\left(\dfrac{-2p}{1-p^2}\right) = 0$	$\dfrac{2}{p(1+p)(1-p^2)}$
13	F₃ from doubly dominant F₂; h and i identified	$(e+h)\left(\dfrac{2}{p}\right) + (f+g)\left[\dfrac{1-2p}{p(1-p)}\right] + i\left(\dfrac{2}{p-1}\right) - (e+f+g+h+i)\left(\dfrac{2p}{2+p^2}\right) = 0$	$\dfrac{4(2+2p-p^2)}{p(1-p)(2+p^2)^2}$
14	F₃ from doubly dominant F₂; h and i not separated	$e\left(\dfrac{2}{p}\right) + (f+g)\left[\dfrac{1-2p}{p(1-p)}\right] + (h+i)\left[\dfrac{2(2p-1)}{1-2p+2p^2}\right] - (e+f+g+h+i)\left(\dfrac{2p}{2+p^2}\right) = 0$	$\dfrac{4(2-6p+3p^2+4p^3)}{p(1-p)(2+p^2)^2(1-2p+2p^2)}$
15	Separation of h and i	$h\left(\dfrac{2}{p}\right) + i\left(\dfrac{2}{p-1}\right) - (h+i)\left[\dfrac{2(2p-1)}{1-2p+2p^2}\right] = 0$	$\dfrac{4}{(1-2p+2p^2)^2}$
16	1:2:1 within recessive class	$l\left(\dfrac{2}{p-1}\right) + m\left[\dfrac{1-2p}{p(1-p)}\right] + n\left(\dfrac{2}{p}\right) = 0$	$\dfrac{1}{2p(1-p)}$
17	1:2:1 within dominant class	$(e+f)\left[\dfrac{2(1-p)}{p(2-p)}\right] + (g+h+i)\left(\dfrac{2p-1}{1-p+p^2}\right) + (j+k)\left(\dfrac{-2p}{1-p^2}\right) = 0$	$\dfrac{p^2}{1-p^2} + \dfrac{(1-2p)^2}{2(1-p+p^2)} + \dfrac{(1-p)^2}{p(2-p)}$
18	3:1/2:1 (6:3:2:1)	$(e+f)\left[\dfrac{2(1-p)}{p(2-p)}\right] + (g+h+i)\left(\dfrac{2p-1}{1-p+p^2}\right) + j\left(\dfrac{2}{p-1}\right) + k\left[\dfrac{1-2p}{p(1-p)}\right] = 0$	$1 + \dfrac{(1-p)^2}{2(1-p+p^2)} + \dfrac{(1-2p)^2}{2(1-p+p^2)} + \dfrac{(1-2p)^2}{2p(1-p)}$
19	2:1/1:2:1 (2:4:2:1:2:1)	$e\left(\dfrac{2}{p}\right) + (f+g+k)\left[\dfrac{1-2p}{p(1-p)}\right] + (h+i)\left[\dfrac{2(2p-1)}{1-2p+2p^2}\right] + j\left(\dfrac{2}{p-1}\right) = 0$	$\dfrac{3-10p+10p^2}{2p(1-p)(1-2p+2p^2)}$
20	Backcross to triple recessive‖	$o\left(\dfrac{1}{p}\right) + (q+r+s)\left(\dfrac{1}{p-2}\right) + t\left(\dfrac{1}{p-1}\right) + (u+v+w)\left(\dfrac{1}{1+p}\right) = 0$	$\dfrac{1+2p-2p^2}{2p(1-p^2)(2-p)}$
21	3:1/9:7 (27:21:9:7)	$(a+b')\left(\dfrac{2p}{2+p^2}\right) + c'\left(\dfrac{2p-1}{1-p+p^2}\right) + (d'+e')\left(\dfrac{-2p}{2-p^2}\right) + f'\left(\dfrac{6p}{1+3p^2}\right) = 0$	$\dfrac{3p^2(5+2p^2-4p^4)}{(2+p^2)(1-p^2)(2-p^2)(1+3p^2)}$
22	1:2:1/9:7	$a'\left[\dfrac{2(1-p)}{p(2-p)}\right] + b'\left(\dfrac{2p-1}{1-p+p^2}\right) + c'\left(\dfrac{-2p}{1-p^2}\right) + d'\left[\dfrac{6(p-1)}{4-6p+3p^2}\right]$ $+ e'\left[\dfrac{3(1-2p)}{1+3p-3p^2}\right] + f'\left(\dfrac{6p}{1+3p^2}\right) = 0$	$\dfrac{3}{8}\left[\dfrac{2(1-p)^2}{p(2-p)} + \dfrac{(1-2p)^2}{1-p+p^2} + \dfrac{2p^2}{1-p^2}\right.$ $\left. + \dfrac{6(1-p)^2}{4-6p+3p^2} + \dfrac{3(1-2p)^2}{1+3p-3p^2} + \dfrac{6p^2}{1+3p^3}\right]$

TABLE 6 (*Concluded*)

Equation or formula	Type of data	Estimation equation	Information (i_p)
23	3:1/15:1 (45:15:3:1)	$(g'+h'+j'+k'+m'+n')\left(\dfrac{2p}{11+p^2}\right) + (i'+l'+o')\left(\dfrac{-2p}{4-p^2}\right) + (q'+r')\left(\dfrac{-2p}{1-p^2}\right) + s'\left(\dfrac{2}{p}\right) = 0$	$\dfrac{11+2p^2-4p^4}{(11+p^2)(4-p^2)(1-p^2)}$
24	1:2:1/15:1	$(g'+j'+m')\left[\dfrac{2(1-p)}{3+2p-p^2}\right] + (h'+k'+n')\left(\dfrac{2p-1}{4-p+p^2}\right) + (i'+l'+o')\left(\dfrac{-2p}{4-p^2}\right) + q'\left(\dfrac{2}{p-1}\right) + r'\left[\dfrac{1-2p}{p(1-p)}\right] + s'\left(\dfrac{2}{p}\right) = 0$	$1/8\left[4 + \dfrac{2(1-p)^2}{3+2p-p^2} + \dfrac{(1-2p)^2}{4-p+p^2} + \dfrac{2p^2}{4-p^2} + \dfrac{(1-2p)^2}{p(1-p)}\right]$
25	3:1/7:4:4:1	$(g'+h')\left[\dfrac{2(1-p)}{1+2p-p^2}\right] + i'\left[\dfrac{6(p-1)}{4-6p+3p^2}\right] + (j'+k')\left(\dfrac{2p-1}{1-p+p^2}\right) + v\left[\dfrac{1-2p}{p(1-p)}\right] + (m'+n')\left(\dfrac{1}{p-2}\right) + o'\left(\dfrac{1}{p}\right) + (q'+r')\left(\dfrac{-2p}{1-p^2}\right) + s'\left(\dfrac{2}{p}\right) = 0$	$1/8\left[2 + \dfrac{6(1-p)^2}{1+2p-p^2} + \dfrac{18(1-p)^2}{4-6p+3p^2} + \dfrac{2(1-2p)^2}{1-p+p^2} + \dfrac{2(1-2p)^2}{p(1-p)} + \dfrac{1}{2-p} + \dfrac{1}{p} + \dfrac{2p^2}{1-p^2}\right]$
26	1:2:1/7:4:4:1	$g'\left(\dfrac{6p}{1+3p^2}\right) + h'\left[\dfrac{3(1-2p)}{1+3p-3p^2}\right] + i'\left[\dfrac{6(p-1)}{4-6p+3p^2}\right] + (i'+l'+r')\left[\dfrac{1-2p}{p(1-p)}\right] + k'\left[\dfrac{2(2p-1)}{1-2p+2p^2}\right] + m'\left(\dfrac{1}{p-1}\right) + n'(0) + o'\left(\dfrac{1}{p}\right) + q'\left(\dfrac{2}{p-1}\right) + s'\left(\dfrac{2}{p}\right) = 0$	$1/8\left[4 + \dfrac{1}{p} + \dfrac{1}{1-p} + \dfrac{8(1-2p)^2}{1-2p+2p^2} + \dfrac{5(1-2p)^2}{p(1-p)} + \dfrac{18(1-p)^2}{4-6p+3p^2} + \dfrac{9(1-2p)^2}{1+3p-3p^2} + \dfrac{18p^2}{1+3p^2}\right]$
27	3:1/13:3	$(t'+u')\left(\dfrac{2p}{3+p^2}\right) + v'\left(\dfrac{-2p}{4-3p^2}\right) + (w'+x')\left(\dfrac{-2p}{1-p^2}\right) + y'\left(\dfrac{2}{p}\right) = 0$	$\dfrac{3(3+2p^2-4p^4)}{(3+p^2)(1-p^2)(4-3p^2)}$
28	1:2:1/13:3	$t'\left(\dfrac{6(1-p)}{1+6p-3p^2}\right) + u'\left[\dfrac{3(2p-1)}{4-3p+3p^2}\right] + v'\left(\dfrac{-6p}{4-3p^2}\right) + w'\left(\dfrac{2}{p-1}\right) + x'\left[\dfrac{1-2p}{p(1-p)}\right] + y'\left(\dfrac{2}{p}\right) = 0$	$3/8\left[4 + \dfrac{6(1-p)^2}{1+6p-3p^2} + \dfrac{3(1-2p)^2}{4-3p+3p^2} + \dfrac{6p^2}{4-3p^2} + \dfrac{(1-2p)^2}{p(1-p)}\right]$

* Certain types of data are described, for the sake of convenience, by the ratio expected when p = 0.50.

† For duplicate genes the estimation equation is $(a + b + c)\left(\dfrac{-1}{2-p}\right) + d\left(\dfrac{1}{p}\right) = 0$.

‡ 9:6:1 ratio identical.

TABLE 7

SCORES FOR THE SOLUTION OF MAXIMUM LIKELIHOOD EQUATIONS USED IN THE ESTIMATION OF RECOMBINATION VALUES*

$\dfrac{d \log m}{dp}$	0.01	0.02	0.03
$\dfrac{2}{p}$	200.0000000	100.0000000	66.6666667
$\dfrac{2}{p-1}$	−2.0202020	−2.0408163	−2.0618557
$\dfrac{-2p}{1-p^2}$	−0.0200020	−0.0400160	−0.0600540
$\dfrac{2p}{2+p^2}$	0.0099995	0.0199960	0.0299865
$\dfrac{-2p}{2-p^2}$	−0.0100005	−0.0200040	−0.0300135
$\dfrac{2p}{3+p^2}$	0.0066664	0.0133316	0.0199940
$\dfrac{-2p}{4-p^2}$	−0.0050001	−0.0100010	−0.0150034
$\dfrac{1-2p}{p(1-p)}$	98.9898990	48.9795918	32.3024055
$\dfrac{2(1-p)}{p(2-p)}$	99.4974874	49.4949495	32.8257191
$\dfrac{2p-1}{1-p+p^2}$	−0.9897990	−0.9791922	−0.9681739
$\dfrac{2(2p-1)}{1-2p+2p^2}$	−1.9995919	−1.9983347	−1.9961775
$\dfrac{2(p-1)}{3-2p+p^2}$	−0.6644072	−0.6620727	−0.6596620
$\dfrac{2(1-p)}{1+2p-p^2}$	1.9413668	1.8853405	1.8317439
$\dfrac{2(1-p)}{3+2p-p^2}$	0.6556508	0.6448217	0.6341714

* The error in p values calculated from these scores depends upon the population size (n) and the number of scores (s) in the estimation equation. It may be calculated as $E_p = 5ns \times 10^{-8}$.

Value of p

0.04	0.05	0.06	0.07	0.08	0.09	0.10
50.0000000	40.0000000	33.3333333	28.5714286	25.0000000	22.2222222	20.0000000
−2.0833333	−2.1052632	−2.1276596	−2.1505376	−2.1739130	−2.1978022	−2.2222222
−0.0801282	−0.1002506	−0.1204336	−0.1406894	−0.1610306	−0.1814699	−0.2020202
0.0399680	0.0499376	0.0598922	0.0698289	0.0797448	0.0896370	0.0995025
−0.0400320	−0.0500626	−0.0601082	−0.0701719	−0.0802568	−0.0903660	−0.1005025
0.0266525	0.0333056	0.0399521	0.0465906	0.0532198	0.0598384	0.0664452
−0.0200080	−0.0250156	−0.0300270	−0.0350429	−0.0400641	−0.0450913	−0.0501253
23.9583333	18.9473684	15.6028369	13.2104455	11.4130435	10.0122100	8.8888889
24.4897959	19.4871795	16.1512027	13.7675796	11.9791667	10.5875509	9.4736842
−0.9567387	−0.9448819	−0.9325986	−0.9198845	−0.9067358	−0.8931489	−0.8791209
−1.9930676	−1.9889503	−1.9837692	−1.9774660	−1.9699812	−1.9612533	−1.9512195
−0.6571742	−0.6546081	−0.6519628	−0.6492373	−0.6464306	−0.6435416	−0.6405694
1.7804154	1.7312073	1.6839842	1.6386221	1.5950069	1.5530335	1.5126050
0.6237006	0.6133979	0.6032602	0.5932825	0.5834602	0.5737886	0.5642633

TABLE 7—(*Continued*)

$\dfrac{d \log m}{dp}$	0.11	0.12	0.13
$\dfrac{2}{p}$	18.1818182	16.6666667	15.3846154
$\dfrac{2}{p-1}$	-2.2471910	-2.2727273	-2.2988506
$\dfrac{-2p}{1-p^2}$	-0.2226946	-0.2435065	-0.2644695
$\dfrac{2p}{2+p^2}$	0.1093385	0.1191422	0.1289107
$\dfrac{-2p}{2-p^2}$	-0.1106696	-0.1208703	-0.1311079
$\dfrac{2p}{3+p^2}$	0.0730387	0.0796178	0.0861812
$\dfrac{-2p}{4-p^2}$	-0.0551669	-0.0602168	-0.0652758
$\dfrac{1-2p}{p(1-p)}$	7.9673136	7.1969697	6.5428824
$\dfrac{2(1-p)}{p(2-p)}$	8.5618086	7.8014184	7.1575483
$\dfrac{2p-1}{1-p+p^2}$	-0.8646492	-0.8497317	-0.8343669
$\dfrac{2(2p-1)}{1-2p+2p^2}$	-1.9398160	-1.9269777	-1.9126389
$\dfrac{2(p-1)}{3-2p+p^2}$	-0.6375130	-0.6343714	-0.6311437
$\dfrac{2(1-p)}{1+2p-p^2}$	1.4736319	1.4360313	1.3997265
$\dfrac{2(1-p)}{3+2p-p^2}$	0.5548801	0.5456349	0.5365237

Value of p

0.14	0.15	0.16	0.17	0.18	0.19	0.20
14.2857143	13.3333333	12.5000000	11.7647059	11.1111111	10.5263158	10.0000000
−2.3255814	−2.3529412	−2.3809524	−2.4096386	−2.4290244	−2.4691358	−2.5000000
−0.2855977	−0.3069054	−0.3284072	−0.3501184	−0.3720546	−0.3942318	−0.4166667
0.1386413	0.1483313	0.1579779	0.1675785	0.1771305	0.1866313	0.1960784
−0.1413856	−0.1517067	−0.1620746	−0.1724925	−0.1829640	−0.1934925	−0.2040816
0.0927275	0.0992556	0.1057641	0.1122520	0.1187178	0.1251606	0.1315789
−0.0703447	−0.0754243	−0.0805153	−0.0856186	−0.0907350	−0.0958652	−0.1010101
5.9800665	5.4901161	5.0595238	4.6775337	4.3360434	4.0285900	3.7500000
6.6052227	6.1261261	5.7065217	5.3359049	5.0061050	4.7106717	4.4444444
−0.8185539	−0.8022923	−0.7855823	−0.7684247	−0.7508212	−0.7327739	−0.7142857
−1.8967334	−1.8791946	−1.8599562	−1.8389524	−1.8161180	−1.7913898	−1.7647059
−0.6278289	−0.6244261	−0.6209344	−0.6173528	−0.6136806	−0.6099168	−0.6060606
1.3646461	1.3307241	1.2978986	1.2661124	1.2353118	1.2054468	1.1764706
0.5275426	0.5186880	0.5099563	0.5013440	0.4928477	0.4844642	0.4761905

TABLE 7—(*Continued*)

$\dfrac{d \log m}{dp}$	0.21	0.22	0.23
$\dfrac{2}{p}$	9.5238095	9.0909091	8.6956522
$\dfrac{2}{p-1}$	−2.5316756	−2.5641026	−2.5974026
$\dfrac{-2p}{1-p^2}$	−0.4393765	−0.4623792	−0.4856932
$\dfrac{2p}{2+p^2}$	0.2054694	0.2148018	0.2240733
$\dfrac{-2p}{2-p^2}$	−0.2147349	−0.2254560	−0.2362488
$\dfrac{2p}{3+p^2}$	0.1379718	0.1443380	0.1506764
$\dfrac{-2p}{4-p^2}$	−0.1061705	−0.1113473	−0.1165413
$\dfrac{1-2p}{p(1-p)}$	3.4960820	3.2634033	3.0491248
$\dfrac{2(1-p)}{p(2-p)}$	4.2032455	3.9836568	3.7828543
$\dfrac{2p-1}{1-p+p^2}$	−0.6953603	−0.6760019	−0.6562158
$\dfrac{2(2p-1)}{1-2p+2p^2}$	−1.7360072	−1.7052375	−1.6723444
$\dfrac{2(p-1)}{3-2p+p^2}$	−0.6021112	−0.5980678	−0.5939296
$\dfrac{2(1-p)}{1+2p-p^2}$	1.1483393	1.1210118	1.0944496
$\dfrac{2(1-p)}{3+2p-p^2}$	0.4680233	0.4599599	0.4519973

Value of p

0.24	0.25	0.26	0.27	0.28	0.29	0.30
8.3333333	8.0000000	7.6923077	7.4074074	7.1428571	6.8965517	6.6666667
−2.6315789	−2.6666667	−2.7027027	−2.7397260	−2.7777778	−2.8169014	−2.8571429
−0.5093379	−0.5333333	−0.5577006	−0.5824614	−0.6076389	−0.6332569	−0.6593407
0.2332815	0.2424242	0.2514993	0.2605046	0.2694380	0.2782976	0.2870813
−0.2471170	−0.2580645	−0.2690954	−0.2802138	−0.2914238	−0.3027298	−0.3141361
0.1569859	0.1632653	0.1695136	0.1757298	0.1819127	0.1880613	0.1941748
−0.1217533	−0.1269841	−0.1322348	−0.1375061	−0.1427989	−0.1481141	−0.1534527
2.8508772	2.6666667	2.4948025	2.3338407	2.1825397	2.0398252	1.9047619
3.5984848	3.4285714	3.2714412	3.1255669	2.9900332	2.8634805	2.7450980
−0.6360078	−0.6153846	−0.5943536	−0.5729232	−0.5511022	−0.5289006	−0.5063291
−1.6372796	−1.6000000	−1.5604681	−1.5186530	−1.4745308	−1.4280857	−1.3793103
−0.5896958	−0.5853659	−0.5809389	−0.5764144	−0.5717916	−0.5670700	−0.5622490
1.0686164	1.0434783	1.0190030	0.9951605	0.9719222	0.9492613	0.9271523
0.4441328	0.4363636	0.4286873	0.4211012	0.4136029	0.4061901	0.3988604

TABLE 7—(*Continued*)

$\dfrac{d \log m}{dp}$	0.31	0.32	0.33
$\dfrac{2}{p}$	6.4516129	6.2500000	6.0606061
$\dfrac{2}{p-1}$	−2.8985507	−2.9411765	−2.9850746
$\dfrac{-2p}{1-p^2}$	−0.6859166	−0.7130125	−0.7406576
$\dfrac{2p}{2+p^2}$	0.2957874	0.3044140	0.3129594
$\dfrac{-2p}{2-p^2}$	−0.3256474	−0.3372681	−0.3490032
$\dfrac{2p}{3+p^2}$	0.2002519	0.2062919	0.2122937
$\dfrac{-2p}{4-p^2}$	−0.1588155	−0.1642036	−0.1696179
$\dfrac{1-2p}{p(1-p)}$	1.7765311	1.6544118	1.5377657
$\dfrac{2(1-p)}{p(2-p)}$	2.6340905	2.5297619	2.4315006
$\dfrac{2p-1}{1-p+p^2}$	−0.4833991	−0.4601227	−0.4365130
$\dfrac{2(2p-1)}{1-2p+2p^2}$	−1.3282069	−1.2747875	−1.2190749
$\dfrac{2(p-1)}{3-2p+p^2}$	−0.5573281	−0.5523067	−0.5471845
$\dfrac{2(1-p)}{1+2p-p^2}$	0.9055712	0.8844953	0.8639030
$\dfrac{2(1-p)}{3+2p-p^2}$	0.3916116	0.3844414	0.3773479

Value of p						
0.34	0.35	0.36	0.37	0.38	0.39	0.40
5.8823529	5.7142857	5.5555556	5.4054054	5.2631579	5.1282051	5.0000000
−3.0303030	−3.0769231	−3.1250000	−3.1746032	−3.2258065	−3.2786885	−3.3333333
−0.7688829	−0.7977208	−0.8272059	−0.8573746	−0.8882655	−0.9199198	−0.9523810
0.3214218	0.3297998	0.3380917	0.3462960	0.3544115	0.3624367	0.3703704
−0.3608576	−0.3728362	−0.3849444	−0.3971875	−0.4095710	−0.4221008	−0.4347826
0.2182565	0.2241793	0.2300613	0.2359017	0.2416995	0.2474541	0.2531646
−0.1750592	−0.1805287	−0.1860273	−0.1915560	−0.1971159	−0.2027080	−0.2083333
1.4260250	1.3186813	1.2152778	1.1154011	1.0186757	0.9247583	0.8333333
2.3387668	2.2510823	2.1680217	2.0892058	2.0142950	1.9429846	1.8750000
−0.4125838	−0.3883495	−0.3638254	−0.3390273	−0.3139717	−0.2886760	−0.2631579
−1.1611030	−1.1009174	−1.0385757	−0.9741476	−0.9077156	−0.8393743	−0.7692308
−0.5419609	−0.5366357	−0.5312085	−0.5256790	−0.5200470	−0.5143122	−0.5084746
0.8437740	0.8240887	0.8048290	0.7859772	0.7675167	0.7494318	0.7317073
0.3703288	0.3633823	0.3565062	0.3496989	0.3429583	0.3362827	0.3296703

TABLE 7—(*Continued*)

$\dfrac{d \log m}{dp}$	0.41	0.42	0.43
$\dfrac{2}{p}$	4.8780488	4.7619048	4.6511628
$\dfrac{2}{p-1}$	-3.3898305	-3.4482759	-3.5087719
$\dfrac{-2p}{1-p^2}$	-0.9856954	-1.0199126	-1.0550853
$\dfrac{2p}{2+p^2}$	0.3782113	0.3859585	0.3936107
$\dfrac{-2p}{2-p^2}$	-0.4476227	-0.4606273	-0.4738031
$\dfrac{2p}{3+p^2}$	0.2588302	0.2644503	0.2700242
$\dfrac{-2p}{4-p^2}$	-0.2139931	-0.2196882	-0.2254200
$\dfrac{1-2p}{p(1-p)}$	0.7441091	0.6568145	0.5711954
$\dfrac{2(1-p)}{p(2-p)}$	1.8100936	1.7480410	1.6886387
$\dfrac{2p-1}{1-p+p^2}$	-0.2374357	-0.2115283	-0.1854550
$\dfrac{2(2p-1)}{1-2p+2p^2}$	-0.6974041	-0.6240250	-0.5492350
$\dfrac{2(p-1)}{3-2p+p^2}$	-0.5025340	-0.4964903	-0.4903437
$\dfrac{2(1-p)}{1+2p-p^2}$	0.7143290	0.6972830	0.6805564
$\dfrac{2(1-p)}{3+2p-p^2}$	0.3231195	0.3166285	0.3101956

Value of p

0.44	0.45	0.46	0.47	0.48	0.49	0.50
4.5454545	4.4444444	4.3478261	4.2553191	4.1666667	4.0816327	4.0000000
−3.5714286	−3.6363636	−3.7037037	−3.7735849	−3.8461538	−3.9215686	−4.0000000
−1.0912698	−1.1285266	−1.1669203	−1.2065203	−1.2474012	−1.2896434	−1.3333333
0.4011670	0.4086266	0.4159884	0.4232518	0.4304161	0.4374805	0.4444444
−0.4871568	−0.5006954	−0.5144263	−0.5283570	−0.5424955	−0.5568498	−0.5714286
0.2755511	0.2810304	0.2864616	0.2918439	0.2971768	0.3024598	0.3076923
−0.2311896	−0.2379980	−0.2428466	−0.2487365	−0.2546689	−0.2606452	−0.2666667
0.4870130	0.4040404	0.3220612	0.2408671	0.1602564	0.0800320	0.0000000
1.6317016	1.5770609	1.5245624	1.4740648	1.4254386	1.3785647	1.3333333
−0.1592357	−0.1328904	−0.1064396	−0.0799041	−0.0533049	−0.0266631	0.0000000
−0.4731861	−0.3960396	−0.3179650	−0.2391391	−0.1597444	−0.0799680	0.0000000
−0.4840941	−0.4777416	−0.4712864	−0.4647288	−0.4580691	−0.4513075	−0.4444444
0.6641366	0.6480118	0.6321705	0.6166017	0.6012951	0.5862406	0.5714286
0.3038194	0.2974983	0.2912307	0.2850152	0.2788503	0.2727346	0.2666667

TABLE 7—(*Concluded*)

$\dfrac{d \log m}{dp}$	0.51	0.52	0.53
$\dfrac{2}{p}$	3.9215686	3.8461538	3.7735849
$\dfrac{2}{p-1}$	-4.0816327	-4.1666667	-4.2553191
$\dfrac{-2p}{1-p^2}$	-1.3785647	-1.4254386	-1.4740648
$\dfrac{2p}{2+p^2}$	0.4513075	0.4580691	0.4647288
$\dfrac{-2p}{2-p^2}$	-0.5862406	-0.6012951	-0.6166017
$\dfrac{2p}{3+p^2}$	0.3128738	0.3180039	0.3230821
$\dfrac{-2p}{4-p^2}$	-0.2727346	-0.2788503	-0.2850152
$\dfrac{1-2p}{p(1-p)}$	-0.0800320	-0.1602564	-0.2408671
$\dfrac{2(1-p)}{p(2-p)}$	1.2896434	1.2474012	1.2065203
$\dfrac{2p-1}{1-p+p^2}$	0.0266631	0.0533049	0.0799041
$\dfrac{2(2p-1)}{1-2p+2p^2}$	0.0799680	0.1597444	0.2391391
$\dfrac{2(p-1)}{3-2p+p^2}$	-0.4374805	-0.4304161	-0.4232518
$\dfrac{2(1-p)}{1+2p-p^2}$	0.5568498	0.5424955	0.5283570
$\dfrac{2(1-p)}{3+2p-p^2}$	0.2606452	0.2546689	0.2487365

Value of p

0.54	0.55	0.56	0.57
3.7037037	3.6363636	3.5714286	3.5087719
−4.3478261	−4.4444444	−4.5454545	−4.6511628
−1.5245624	−1.5770609	−1.6317016	−1.6886387
0.4712864	0.4777416	0.4840941	0.4903437
−0.6321705	−0.6480118	−0.6641366	−0.6805564
0.3281079	0.3330810	0.3380010	0.3428675
−0.2912307	−0.2974983	−0.3038194	−0.3101956
−0.3220612	−0.4040404	−0.4870130	−0.5711954
1.1669203	1.1285266	1.0912698	1.0550853
0.1064396	0.1328904	0.1592357	0.1854550
0.3179650	0.3960396	0.4731861	0.5492350
−0.4159884	−0.4086266	−0.4011670	−0.3936107
0.5144263	0.5006954	0.4871568	0.4738031
0.2428466	0.2369980	0.2311896	0.2254200

TABLE 8

INFORMATION PER F_2 INDIVIDUAL OR F_3 FAMILY FOR SEVERAL TYPES OF GENETIC SITUATIONS AT VARIOUS RECOMBINATION VALUES*

For-mula	Type of data	Link-age phase	Value of p									
			0.01	0.02	0.03	0.04	0.05	0.06	0.07	0.08	0.09	0.10
1	F_2, complete classi-fication†		202.020	102.041	68.364	52.083	42.105	35.461	30.722	27.174	24.420	22.222
3	Backcross‡ (3 : 1)	R	50.251	25.252	16.920	12.755	10.256	8.591	7.402	6.510	5.817	5.263
		C	1.000	1.000	1.001	1.002	1.003	1.004	1.005	1.006	1.008	1.010
4	F_2, 1:2:1:2:4:2:1:2:1		199.980	99.959	66.605	49.900	39.895	33.207	28.423	24.829	22.028	19.783
5	F_2, 3 : 6 : 3 : 1 : 2 : 1		100.241	75.247	31.559	24.947	20.210	16.870	14.483	12.691	11.297	10.180
6	F_2, 9 : 3 : 3 : 1	R	1.000	1.001	1.002	1.004	1.006	1.009	1.012	1.016	1.020	1.025
		C	99.831	49.829	33.161	24.826	19.824	16.489	14.106	12.318	10.927	9.815
8	F_2, 13 : 3	R	0.000	0.001	0.001	0.002	0.003	0.005	0.007	0.009	0.011	0.013
		C	49.498	24.495	16.159	11.990	9.348	7.819	6.626	5.730	5.034	4.476
9	F_2, 9 : 3 : 4	R	0.000	0.001	0.001	0.002	0.004	0.005	0.007	0.010	0.012	0.015
		C	49.580	24.577	16.240	12.071	9.567	7.897	6.704	5.808	5.110	4.551
10	F_2, 15 : 1	R	1.000	1.000	1.000	1.000	1.001	1.001	1.001	1.002	1.002	1.003
		C	1.325	1.316	1.308	1.299	1.291	1.284	1.276	1.268	1.261	1.254
11	F_2, 9 : 7	R	0.000	0.000	0.001	0.002	0.003	0.004	0.005	0.006	0.008	0.010
		C	1.290	1.248	1.208	1.120	1.133	1.098	1.064	1.031	0.999	0.969
12	F_3 from singly dominant F_2	R	198.040	98.078	64.783	48.154	38.191	31.560	26.834	23.297	20.554	18.365
		C	51.014	26.028	17.709	13.558	11.073	9.422	8.248	7.371	6.694	6.156
13	F_3 from doubly dominant F_2; h and i separated	R	204.025	104.022	70.696	54.039	44.048	37.390	32.637	29.075	26.305	24.092
		C	136.480	69.850	47.665	36.591	29.963	25.557	22.422	20.081	18.270	16.830
14	F_3 from doubly dominant F_2; h and i not sepa-rated	R	199.929	99.857	66.451	49.709	39.633	32.890	28.050	24.399	21.541	19.238
		C	133.742	67.037	44.776	33.625	26.917	22.430	19.220	16.785	14.887	13.358
15	Separation of h and i		4.163	4.333	4.510	4.693	4.884	5.081	5.287	5.500	5.721	5.949
16	1 : 2 : 1 within re-cession class		50.505	25.510	15.182	12.760	10.526	8.865	7.680	6.793	6.105	5.556
17	1 : 2 : 1 within dominant class		49.736	24.723	16.376	12.186	9.684	8.005	6.802	5.898	5.192	4.625
18	3 : 1/2 : 1 (6 : 3 : 2 : 1)	R	99.241	49.233	32.558	23.945	19.208	15.867	13.478	11.685	10.289	9.170
		C	49.990	24.981	16.638	12.192	9.954	8.279	7.081	6.181	5.479	4.917
19	2 : 1/1 : 2 : 1		149.475	74.449	49.423	36.115	29.369	24.341	20.742	18.035	15.923	14.228
20	Backcross to triple recessive		25.626	13.126	8.961	6.878	5.629	4.797	4.203	3.758	3.413	3.137
21	3 : 1/9 : 7	R	0.000	0.002	0.003	0.006	0.009	0.013	0.018	0.024	0.030	0.037
		C	38.466	19.682	13.400	10.245	8.340	7.061	6.141	5.444	4.897	4.455
22	1 : 2 : 1/9 : 7		38.911	20.079	13.821	10.548	8.614	7.301	6.350	5.626	5.054	4.589
23	3 : 1/15 : 1	R	0.250	0.250	0.250	0.251	0.251	0.251	0.252	0.252	0.253	0.253
		C	12.664	6.412	4.327	3.283	2.656	2.237	1.938	1.713	1.537	1.396
24	1 : 2 : 1/15 : 1		12.737	6.485	4.400	3.357	2.730	2.312	2.013	1.788	1.613	1.473
25	3 : 1/7 : 4 : 4 : 1	R	38.588	19.803	13.519	10.226	8.455	7.192	6.253	5.555	5.007	4.564
		C	37.308	18.554	12.301	9.637	7.297	6.046	5.152	4.483	3.963	3.548
26	1 : 2 : 1/7 : 4 : 4 : 1	R	75.868	38.803	26.242	19.935	16.131	13.580	11.747	10.363	9.279	8.405
		C	75.459	37.946	25.432	19.169	14.906	12.893	11.094	9.743	8.689	7.844
27	3 : 1/13 : 3	R	0.750	0.751	0.751	0.753	0.754	0.756	0.758	0.760	0.763	0.766
		C	39.954	21.053	14.668	11.421	9.437	8.087	7.104	6.352	5.755	5.268
28	1 : 2 : 1/13 : 3		40.232	21.329	14.959	11.690	9.703	8.352	7.367	6.612	6.014	5.526

* The error in σ_p calculated from 3 decimal place tables of i_p is a function of population size (n) and the i_p value such that $E_{\sigma p} = 5 \times 10^{-4} n^{-1/2} i_p^{-3/2}$.
† Formula 2 equals one half of formula 1.
‡ Values for formula 7 are identical except that coupling and repulsion are reversed; thus at $p = 0.01$ the repulsion phase value for formula 7 is 1.000 and the coupling phase value 50.251.

For-mula	Type of data	Link-age phase	Value of p									
			0.11	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.20
1	F_2, complete classi-fication.........		20.429	18.939	17.683	16.611	15.686	14.881	14.174	13.550	12.995	12.500
3	Backcross (3 : 1)...	R	4.810	4.433	4.114	3.840	3.604	3.397	3.214	3.053	2.870	2.778
		C	1.012	1.015	1.017	1.020	1.023	1.026	1.030	1.033	1.037	1.042
4	F_2, 1:2:1:2:4:2:1:2:1..		17.942	16.404	15.099	13.977	13.002	12.146	11.388	10.712	10.106	9.559
5	F_2, 3 : 6 : 3 : 1 : 2 : 1		9.267	8.505	7.860	7.308	6.829	6.410	6.041	5.714	5.421	5.159
6	F_2, 9 : 3 : 3 : 1.....	R	1.031	1.036	1.043	1.050	1.057	1.065	1.074	1.083	1.093	1.103
		C	8.904	8.144	7.502	6.950	6.473	6.054	5.685	5.357	5.063	4.798
8	F_2, 13 : 3..........	R	0.016	0.019	0.023	0.026	0.030	0.035	0.039	0.044	0.049	0.055
		C	4.019	3.638	3.315	3.038	2.798	2.587	2.401	2.236	2.087	1.954
9	F_2, 9 : 3 : 4........	R	0.018	0.022	0.026	0.030	0.034	0.039	0.044	0.049	0.055	0.061
		C	4.094	3.712	3.388	3.110	2.869	2.658	2.471	2.304	2.155	2.020
10	F_2, 15:1	R	1.003	1.004	1.004	1.005	1.006	1.006	1.007	1.008	1.009	1.010
		C	1.247	1.240	1.233	1.227	1.220	1.214	1.208	1.202	1.195	1.190
11	F_2, 9:7	R	0.012	0.014	0.017	0.020	0.023	0.026	0.029	0.032	0.036	0.040
		C	0.939	0.911	0.883	0.857	0.831	0.806	0.782	0.758	0.735	0.705
12	F_3 from singly dominant F_2....	R	16.581	15.098	13.849	12.782	11.861	11.059	10.355	9.732	9.177	8.681
		C	5.719	5.359	5.057	4.802	4.583	4.395	4.233	4.091	3.967	3.858
13	F_3 from doubly dominant F_2; h and i separated..	R	22.282	20.776	19.502	18.411	17.468	16.643	15.916	15.271	14.695	14.177
		C	15.660	14.675	13.881	13.193	12.603	12.093	11.649	11.261	10.919	10.618
14	F_3 from doubly dominant F_2; h and i not sepa-rated............	R	17.338	15.741	14.376	13.194	12.158	11.241	10.423	9.686	9.019	8.410
		C	12.097	11.037	10.131	9.346	8.659	8.049	7.504	7.014	6.568	6.161
15	Separation of h and i............		6.185	6.429	6.680	6.940	7.207	7.481	7.763	8.052	8.348	8.651
16	1 : 2 : 1 within re-cessive class.....		5.107	4.735	4.421	4.153	3.922	3.720	3.544	3.388	3.249	3.125
17	1 : 2 : 1 within dominant class..		4.159	3.770	3.439	3.155	2.907	2.690	2.498	2.326	2.172	2.034
18	3 : 1/2 : 1......... (6 : 3 : 2 : 1)	R	8.254	7.490	6.843	6.288	5.806	5.346	5.012	4.680	4.384	4.117
		C	4.457	4.072	3.747	3.468	3.225	3.014	2.827	2.661	2.513	2.381
19	2 : 1/1 : 2 : 1.......		12.835	11.669	10.678	9.824	9.080	8.425	7.844	7.325	6.857	6.434
20	Backcross to triple recessive........		2.911	2.724	2.565	2.430	2.313	2.212	2.122	2.043	1.973	1.910
21	3 : 1/9 : 7..........	R	0.045	0.053	0.062	0.071	0.082	0.092	0.104	0.116	0.128	0.142
		C	4.090	3.782	3.518	3.290	3.089	2.911	2.752	2.610	2.480	2.361
22	1 : 2 : 1/9 : 7......		4.203	3.876	3.596	3.353	3.140	2.951	2.783	2.632	2.496	2.372
23	3 : 1/15 : 1.........	R	0.254	0.255	0.256	0.257	0.258	0.259	0.260	0.261	0.262	0.264
		C	1.281	1.185	1.103	1.033	0.971	0.918	0.870	0.828	0.790	0.756
24	1 : 2 : 1/15 : 1......		1.358	1.262	1.181	1.112	1.052	0.999	0.952	0.911	0.874	0.841
25	3 : 1/7 : 4 : 4 : 1....	R	4.197	3.889	3.625	3.396	3.195	3.018	2.859	2.717	2.588	2.471
		C	3.209	2.927	2.690	2.488	2.314	2.163	2.030	1.914	1.811	1.720
26	1 : 2 : 1/7 : 4 : 4 : 1.	R	7.685	7.081	6.566	6.121	5.733	5.391	5.087	4.814	4.569	4.347
		C	7.150	6.570	6.078	5.655	5.288	4.965	4.679	4.425	4.196	3.990
27	3 : 1/13 : 3.........	R	0.769	0.773	0.777	0.781	0.786	0.791	0.796	0.802	0.808	0.814
		C	4.862	4.517	4.221	3.963	3.735	3.533	3.353	3.190	3.042	2.902
28	1 : 2 : 1/13 : 3......		5.120	4.551	4.478	4.220	3.994	3.793	3.613	3.452	3.306	3.174

TABLE 8—(*Continued*)

For-mula	Type of data	Link-age phase	Value of p									
			0.21	0.22	0.23	0.24	0.25	0.26	0.27	0.28	0.29	0.30
1	F_2, complete classification..........		12.055	11.655	11.293	10.965	10.667	10.395	10.147	9.921	9.713	9.524
3	Backcross (3 : 1)...	R	2.660	2.554	2.456	2.367	2.286	2.210	2.141	2.076	2.017	1.961
		C	1.046	1.051	1.056	1.061	1.067	1.073	1.079	1.085	1.092	1.099
4	F_2 1:2:1:2:4:2:1:2:1..		9.062	8.610	8.154	7.816	7.467	7.144	6.846	6.569	6.313	6.076
5	F_2, 3 : 6 : 3 : 1 : 2 : 1		4.922	4.708	4.513	4.335	4.173	4.024	3.888	3.763	3.648	3.542
6	F_2, 9 : 3 : 3 : 1......	R	1.114	1.125	1.141	1.150	1.167	1.178	1.192	1.208	1.224	1.241
		C	4.546	4.341	4.141	3.959	3.791	3.636	3.492	3.359	3.234	3.118
8	F_2, 13 : 3..........	R	0.061	0.067	0.073	0.080	0.087	0.095	0.102	0.111	0.119	0.128
		C	1.832	1.722	1.621	1.524	1.444	1.365	1.292	1.224	1.160	1.101
9	F_2, 9 : 3 : 4........	R	0.068	0.074	0.082	0.089	0.097	0.105	0.114	0.123	0.132	0.142
		C	1.898	1.787	1.685	1.592	1.505	1.425	1.345	1.282	1.218	1.158
10	F_2, 15 : 1..........	R	1.011	1.012	1.013	1.015	1.016	1.017	1.019	1.020	1.021	1.023
		C	1.185	1.179	1.174	1.169	1.164	1.159	1.154	1.149	1.144	1.140
11	F_2, 9 : 7..........	R	0.044	0.048	0.053	0.058	0.063	0.068	0.073	0.079	0.084	0.090
		C	0.691	0.670	0.650	0.628	0.611	0.592	0.574	0.556	0.538	0.521
12	F_3 from singly dominant F_2....	R	8.234	7.831	7.465	7.131	6.827	6.548	6.291	6.055	5.837	5.635
		C	3.763	3.679	3.605	3.540	3.483	3.433	3.390	3.353	3.322	3.295
13	F_3 from doubly dominant F_2; h and i separated..	R	13.710	13.286	12.900	12.548	12.224	11.927	11.652	11.398	11.163	10.945
		C	10.350	10.112	9.901	9.712	9.544	9.393	9.259	9.140	9.034	8.940
14	F_3 from doubly dominant F_2; h and i not separated...........	R	7.853	7.340	6.866	6.427	6.018	5.637	5.281	4.949	4.637	4.346
		C	5.788	5.443	5.123	4.826	4.548	4.289	4.046	3.817	3.602	3.401
15	Separation of h and i............		8.959	9.272	9.591	9.914	10.240	10.569	10.899	11.236	11.561	11.891
16	1 : 2 : 1 within recessive class.....		3.014	2.914	2.823	2.741	2.667	2.599	2.537	2.480	2.428	2.381
17	1 : 2 : 1 within dominant class..		1.908	1.794	1.689	1.594	1.506	1.426	1.351	1.283	1.219	1.161
18	3 : 1/2 : 1.......... (6 : 3 : 2 : 1)	R	3.876	3.657	3.457	3.274	3.106	2.952	2.809	2.678	2.556	2.443
		C	2.262	2.154	2.056	1.968	1.887	1.814	1.747	1.686	1.631	1.581
19	2 : 1/1 : 2 : 1.......		6.048	5.696	5.373	5.075	4.800	4.545	4.309	4.089	3.885	3.695
20	Backcross to triple recessive........		1.862	1.802	1.756	1.714	1.676	1.641	1.610	1.581	1.554	1.530
21	3 : 1/9 : 7..........	R	0.155	0.170	0.184	0.200	0.215	0.230	0.248	0.266	0.283	0.301
		C	2.253	2.153	2.060	1.974	1.893	1.818	1.747	1.681	1.618	1.558
22	1 : 2 : 1/9 : 7.......		2.259	2.158	2.063	1.978	1.899	1.826	1.759	1.697	1.640	1.587
23	3 : 1/15 : 1..........	R	0.265	0.267	0.269	0.270	0.272	0.274	0.276	0.278	0.280	0.283
		C	0.725	0.697	0.670	0.647	0.625	0.604	0.585	0.568	0.551	0.536
24	1 : 2 : 1/15 : 1......		0.812	0.785	0.760	0.738	0.717	0.699	0.682	0.666	0.652	0.638
25	3 : 1/7 : 4 : 4 : 1....	R	2.363	2.265	2.174	2.091	2.013	1.940	1.873	1.804	1.751	1.696
		C	1.639	1.566	1.501	1.443	1.391	1.344	1.302	1.264	1.231	1.201
26	1 : 2 : 1/7 : 4 : 4 : 1.	R	4.083	3.960	3.791	3.634	3.490	3.356	3.232	3.116	3.008	2.908
		C	3.807	3.633	3.477	3.334	3.203	3.082	2.970	2.868	2.772	2.684
27	3 : 1/13 : 3..........	R	0.821	0.828	0.836	0.844	0.852	0.861	0.870	0.880	0.890	0.900
		C	2.784	2.671	2.567	2.470	2.380	2.296	2.218	2.145	2.076	2.012
28	1 : 2 : 1/13 : 3......		3.054	2.944	2.844	2.751	2.666	2.588	2.515	2.448	2.383	2.329

For-mula	Type of data	Link-age phase	Value of p									
			0.31	0.32	0.33	0.34	0.35	0.36	0.37	0.38	0.39	0.40
1	F_2, complete classification.........		9.350	9.191	9.046	8.913	8.791	8.681	8.580	8.489	8.407	8.333
3	Backcross (3 : 1)...	R	1.909	1.860	1.815	1.772	1.732	1.694	1.658	1.624	1.593	1.563
		C	1.106	1.114	1.122	1.131	1.140	1.149	1.159	1.169	1.179	1.190
4	F_2, 1:2:1:2:4:2:1:2:1		5.855	5.650	5.461	5.284	5.121	4.971	4.833	4.707	4.592	4.487
5	F_2, 3 : 6 : 3 : 1 : 2 : 1		3.444	3.350	3.243	3.197	3.127	3.064	3.006	2.953	2.905	2.863
6	F_2, 9 : 3 : 3 : 1.....	R	1.258	1.277	1.296	1.316	1.337	1.359	1.381	1.405	1.429	1.455
		C	3.010	2.908	2.812	2.722	2.638	2.558	2.482	2.410	2.342	2.278
8	F_2, 13 : 3..........	R	0.137	0.147	0.157	0.168	0.179	0.190	0.202	0.215	0.228	0.241
		C	1.046	0.994	0.945	0.899	0.855	0.814	0.775	0.738	0.703	0.670
9	F_2, 9 : 3 : 4........	R	0.152	0.163	0.174	0.185	0.197	0.210	0.223	0.236	0.250	0.265
		C	1.101	1.048	0.998	0.951	0.906	0.864	0.824	0.786	0.749	0.715
10	F_2, 15 : 1..........	R	1.025	1.026	1.028	1.030	1.032	1.033	1.035	1.037	1.040	1.042
		C	1.135	1.131	1.126	1.122	1.118	1.114	1.110	1.106	1.103	1.099
11	F_2, 9 : 7..........	R	0.096	0.103	0.109	0.116	0.123	0.130	0.138	0.145	0.153	0.161
		C	0.505	0.489	0.473	0.457	0.442	0.428	0.413	0.399	0.385	0.372
12	F_3 from singly dominant F_2....	R	5.449	5.275	5.114	4.964	4.824	4.693	4.571	4.458	4.351	4.252
		C	3.274	3.257	3.244	3.234	3.229	3.227	3.229	3.235	3.243	3.255
13	F_3 from doubly dominant F_2; h and i separated..	R	10.742	10.553	10.377	10.213	10.060	9.916	9.782	9.657	9.540	9.431
		C	8.857	8.785	8.722	8.667	8.621	8.583	8.552	8.528	8.510	8.499
14	F_3 from doubly dominant F_2; h and i not separated............	R	4.072	3.816	3.577	3.353	3.144	2.949	2.769	2.602	2.449	2.308
		C	3.211	3.032	2.865	2.708	2.562	2.426	2.299	2.183	2.076	1.980
15	Separation of h and i............		12.217	12.539	12.856	13.166	13.467	13.758	14.038	14.305	14.557	14.793
16	1 : 2 : 1 within recessive class.....		2.338	2.298	2.239	2.228	2.198	2.170	2.145	2.122	2.102	2.083
17	1 : 2 : 1 within dominant class..		1.107	1.052	1.005	0.969	0.929	0.894	0.861	0.831	0.804	0.779
18	3 : 1/2 : 1.......... (6 : 3 : 2 : 1)	R	2.338	2.236	2.121	2.066	1.988	1.915	1.847	1.784	1.726	1.672
		C	1.536	1.495	1.458	1.425	1.396	1.370	1.348	1.329	1.313	1.300
19	2 : 1/1 : 2 : 1.......		3.517	3.352	3.131	3.056	2.924	2.801	2.688	2.585	2.490	2.404
20	Backcross to triple recessive........		1.508	1.487	1.468	1.451	1.436	1.421	1.408	1.397	1.386	1.377
21	3 : 1/9 : 7..........	R	0.320	0.339	0.358	0.378	0.398	0.419	0.440	0.462	0.484	0.508
		C	1.501	1.447	1.396	1.347	1.300	1.255	1.188	1.169	1.129	1.090
22	1 : 2 : 1/9 : 7.......		1.538	1.490	1.447	1.413	1.378	1.346	1.316	1.290	1.265	1.243
23	3 : 1/15 : 1..........	R	0.285	0.287	0.290	0.293	0.296	0.299	0.302	0.305	0.308	0.312
		C	0.521	0.508	0.495	0.483	0.472	0.461	0.451	0.441	0.432	0.423
24	1 : 2 : 1/15 : 1......		0.626	0.615	0.605	0.595	0.587	0.579	0.571	0.565	0.559	0.554
25	3 : 1/7 : 4 : 4 : 1....	R	1.644	1.595	1.535	1.506	1.466	1.428	1.392	1.358	1.327	1.297
		C	1.174	1.151	1.115	1.112	1.096	1.083	1.072	1.063	1.056	1.052
26	1 : 2 : 1/7 : 4 : 4 : 1.	R	2.814	2.727	2.646	2.570	2.499	2.433	2.372	2.316	2.264	2.222
		C	2.602	2.535	2.456	2.392	2.332	2.278	2.228	2.183	2.142	2.106
27	3 : 1/13 : 3..........	R	0.911	0.923	0.935	0.947	0.960	0.974	0.988	1.002	1.017	1.033
		C	1.951	1.893	1.839	1.770	1.739	1.693	1.649	1.607	1.568	1.530
28	1 : 2 : 1/13 : 3......		2.276	2.227	2.182	2.141	2.103	2.068	2.035	2.006	1.980	1.956

TABLE 8—(*Concluded*)

For-mula	Type of data	Link-age phase	Value of p									
			0.41	0.42	0.43	0.44	0.45	0.46	0.47	0.48	0.49	0.50
1	F_2, complete classification..........		8.268	8.210	8.160	8.117	8.081	8.052	8.029	8.009	8.003	8.000
3	Backcross (3 : 1)....	R	1.534	1.507	1.481	1.457	1.434	1.412	1.391	1.371	1.352	1.333
		C	1.202	1.214	1.227	1.240	1.254	1.268	1.284	1.299	1.316	1.333
4	F_2, 1:2:1:2:4:2:1:2:1..		4.393	4.310	4.237	4.174	4.120	4.077	4.043	4.019	4.005	4.000
5	F_2, 3 : 6 : 3 : 1 : 2 : 1		2.824	2.791	2.761	2.736	2.714	2.697	2.684	2.674	2.669	2.667
6	F_2, 9 : 3 : 3 : 1.....	R	1.482	1.510	1.538	1.568	1.598	1.632	1.667	1.702	1.739	1.778
		C	2.216	2.158	2.102	2.049	1.999	1.951	1.904	1.860	1.818	1.778
8	F_2, 13 : 3..........	R	0.255	0.270	0.285	0.301	0.317	0.334	0.352	0.371	0.390	0.410
		C	0.638	0.608	0.579	0.552	0.525	0.500	0.476	0.453	0.431	0.410
9	F_2, 9 : 3 : 4........	R	0.280	0.295	0.311	0.328	0.346	0.364	0.383	0.403	0.423	0.444
		C	0.682	0.651	0.621	0.592	0.565	0.539	0.514	0.490	0.467	0.444
10	F_2, 15 : 1..........	R	1.044	1.046	1.048	1.051	1.053	1.056	1.058	1.061	1.064	1.067
		C	1.095	1.092	1.088	1.085	1.082	1.079	1.076	1.073	1.070	1.067
11	F_2, 9 : 7............	R	0.169	0.178	0.186	0.195	0.205	0.214	0.224	0.234	0.244	0.254
		C	0.359	0.346	0.334	0.322	0.310	0.298	0.287	0.275	0.265	0.254
12	F_3 from singly dominant F_2....	R	4.159	4.072	3.990	3.914	3.843	3.777	3.716	3.658	3.605	3.556
		C	3.270	3.289	3.310	3.335	3.364	3.395	3.430	3.468	3.510	3.556
13	F_3 from doubly dominant F_2; h and i separated..	R	9.329	9.234	9.135	9.063	8.987	8.917	8.852	8.793	8.740	.8.691
		C	8.493	8.487	8.500	8.511	8.528	8.550	8.578	8.610	8.648	8.691
14	F_3 from doubly dominant F_2; h and i not separated............	R	2.181	2.066	1.963	1.873	1.794	1.728	1.674	1.631	1.600	1.580
		C	1.893	1.816	1.750	1.694	1.648	1.613	1.588	1.575	1.572	1.580
15	Separation of h and i............		15.012	15.211	15.391	15.549	15.685	15.797	15.885	15.949	15.987	16.000
16	1 : 2 : 1 within recessive class.....		2.067	2.053	2.040	2.029	2.020	2.013	2.007	2.003	2.001	2.000
17	1 : 2 : 1 within dominant class..		0.757	0.738	0.721	0.707	0.694	0.684	0.677	0.671	0.668	0.667
18	3 : 1/2 : 1.......... (6 : 3 : 2 : 1)	R	1.622	1.576	1.534	1.496	1.461	1.429	1.400	1.375	1.353	1.333
		C	1.290	1.284	1.280	1.279	1.281	1.286	1.293	1.304	1.317	1.333
19	2 : 1/1 : 2 : 1.......		2.326	2.257	2.197	2.144	2.100	2.064	2.036	2.016	2.004	2.000
20	Backcross to triple recessive........		1.368	1.361	1.354	1.348	1.344	1.340	1.337	1.335	1.334	1.333
21	3 : 1/9 : 7..........	R	0.530	0.554	0.578	0.602	0.627	0.653	0.679	0.706	0.734	0.762
		C	1.053	1.017	0.981	0.947	0.914	0.882	0.851	0.820	0.791	0.762
22	1 : 2 : 1/9 : 7.......		1.224	1.206	1.191	1.178	1.167	1.159	1.152	1.147	1.144	1.143
23	3 : 1/15 : 1..........	R	0.315	0.319	0.323	0.327	0.331	0.336	0.340	0.345	0.350	0.356
		C	0.415	0.407	0.400	0.392	0.386	0.379	0.373	0.367	0.361	0.356
24	1 : 2 : 1/15 : 1......		0.549	0.545	0.541	0.538	0.535	0.533	0.532	0.530	0.530	0.529
25	3 : 1/7 : 4 : 4 : 1....	R	1.269	1.243	1.219	1.197	1.176	1.157	1.139	1.123	1.108	1.095
		C	1.048	1.047	1.048	1.050	1.053	1.059	1.065	1.074	1.084	1.095
26	1 : 2 : 1/7 : 4 : 4 : 1.	R	2.173	2.134	2.099	2.068	2.041	2.017	1.998	1.983	1.972	1.964
		C	2.074	2.045	2.021	2.001	1.985	1.973	1.965	1.961	1.961	1.964
27	3 : 1/13 : 3..........	R	1.050	1.067	1.084	1.103	1.122	1.142	1.163	1.185	1.207	1.231
		C	1.493	1.459	1.426	1.394	1.364	1.335	1.307	1.281	1.255	1.231
28	1 : 2 : 1/13 : 3......		1.935	1.916	1.899	1.885	1.873	1.863	1.856	1.850	1.847	1.846